

GULF RESEARCH REPORTS

Vol. 7, No. 2
December 1982
ISSN: 0072-9027



Published by the
GULF COAST RESEARCH LABORATORY
Ocean Springs, Mississippi

Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.01

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Recommended Citation

Ogle, J. T., R. W. Heard and J. Sieg. 1982. Tanaidacea (Crustacea: Peracardia) of the Gulf of Mexico. I. Introduction and an Annotated Bibliography of Tanaidacea Previously Reported from the Gulf of Mexico. *Gulf Research Reports* 7 (2): 101-104.
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TANAIDACEA (CRUSTACEA:PERACARIDA) OF THE GULF OF MEXICO.

I. INTRODUCTION AND AN ANNOTATED BIBLIOGRAPHY OF TANAIDACEA PREVIOUSLY REPORTED FROM THE GULF OF MEXICO

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ABSTRACT A brief summary of the biology and a historical review are presented for the Tanaidacea. An annotated bibliography is provided for published reports and records of Tanaidacea from the Gulf of Mexico.

This is the first in a series of publications on the Tanaidacea to be published in this journal. The purpose of this series of papers will be to provide a definitive summary of the tanaidaceans from the Gulf of Mexico. Each of the papers to follow, beginning with this volume (Sieg et al. 1982) will deal with range extensions, redescrptions, and descriptions of new species from the Gulf of Mexico. Terminology used in species descriptions and redescrptions will follow the preferences of the senior author of each paper in the series, but will generally conform to that of Sieg (1980).

The order tanaidacea is a minor group of the Eumalacostracean crustaceans which are characterized by having the carapace fused to the first two thoracomeres with the first thoracopod being a maxilliped and the second thoracopod a cheliped. Because the females brood their young in a marsupium, or brood pouch, they are generally accepted as members of the superorder Peracarida. Tanaidaceans are a cosmopolitan group of infaunal, epibenthic or epifaunal forms occurring from the intertidal to the abyssal zone. The few species reported from freshwater habitats have been shown to be euryhaline marine species (Gardiner 1975, Sieg 1981). Tanaidaceans are small, ranging in length from 1 to 37 mm with an average size of 2-3 mm. Tanaidaceans are normally deposit feeders with detritus and associated organisms probably their main food, although one group (Kalliapseudidae) are filter feeders. The gonads are double. Oviducts open laterally at the base of the fourth pair of pereopods. The vas deferentia have a common vesicula seminalis which is ventromedian on the last thoracic segment. Hermaphroditism including both protandry and protogyny as well as gonochorism can occur and sexual dimorphism is common. The first antennae can differ in the two sexes as can the shape of the head, the mouth parts, the chelipeds, the first pair of pereopods, and less frequently the pleopods and uropods. Females may produce several broods, each preceded by a molt in which external morphology may undergo alteration. The eggs develop in a marsupium formed by one or four pairs of oostegites. Newly hatched larvae lack the first pair of pereopods and the pleopods. The young undergo two larval (Manca) stages and a neuter stage.

Gammarus heteroclitus Viviani, 1904, was probably the first tanaidacean described, but normally *Cancer gammarus talpa* Montagu, 1808, is accepted as the first described species. Leach (1814) placed the latter species in a new genus, *Apseudes*, in the Amphipoda. Milne-Edwards (1828) placed his genus *Rhoea*, equivalent to *Apseudes*, and a new genus *Tanais* in the Isopoda. Dana (1952) created a new group, Anisopoda, to which he assigned the tanaidaceans and certain isopods considering it to be an intermediate group between Isopoda and Amphipoda. Bate (1868) combined the tanaidaceans with certain isopod taxa into a group he called *Isopoda aberrantia*. Sars (1882) placed the tanaidaceans with the Isopoda under the tribe Chelifera. Claus (1888) created an independent order between the Isopoda and Cumacea that he called Anisopoda after the name proposed by Dana (1852). Hansen (1895) agreed with the affinities but suggested the currently used name Tanaidacea for the order. The view of the Tanaidacea as an independent order is generally accepted by most carcinologists; however, Schram (1981) recently suggested that the tanaidaceans are aligned with the spelaogriphaceans and the cumaceans, and he relegated them to suborders of the order Hemicaridea, which together with the order Thermosbaenacea, comprise the cohort Brachycarida. Sieg (1982) did not follow Schram's scheme. He viewed Schram's grouping of the Isopoda and Amphipoda in the order Acaridea as inconsistent with many recent studies on the comparative morphology and anatomy of the Peracarida. He pointed out that if the Acaridea is part of the Arthropoda, the sister group of the Brachycarida, one would have to accept the parallel evolution of the unique brood pouch, a concept that cannot be followed without refuting the large amount of data supporting the monophyletic origin of the Peracarida.

The first published report of Tanaidacea for the Gulf of Mexico was that of Richardson (1905) for *Apseudes propinquus* Richardson, 1902, off the west coast of Florida. It was not until 61 years later that a second record for the order, *Apseudes spinosus* Sars, 1858, was reported by Dawson (1966) from the northern Gulf. Based on personal collections, and published and unpublished reports, Ogle (1977) listed 18 species from the Gulf of Mexico. The species mentioned by Ogle as "*Apseudes* n. sp. being

described from Florida" is now known to be *Halmyrapseudes bahamensis* Băcescu and Guțu, 1974 (Sieg, Heard and Ogle 1982) and the *Zeuxo* sp. is *Z. maledivensis* Sieg, 1980 (Sieg 1980). Tanaidaceans were the third most abundant group of benthonic, macroinvertebrate crustaceans taken in the Mississippi-Alabama-Florida, Bureau of Land Management study conducted during 1975–1978 (R. W. Heard, unpublished data). Tanaidaceans were also the third most abundant crustacean food item taken from deepwater fish by Bright (1970). Members of the order have been taken more commonly in Gulf waters with the increase in sampling programs during the past decade. The lack of tanaidaceans collected in early sampling programs in the Gulf was probably due to inadequate sampling methods employed.

The taxonomy of some groups of tanaidaceans at present is unclear and confusing. This is due to the many morphological changes that a given species can exhibit dependent on sex, age and molt stage, the ignorance of specific charac-

ters within each taxa, and upon the uncertain position of the group when it was first established. At present there are four suborders of the order Tanaidacea, one of which, the Anthracoridomorpha, is represented only by fossils (Sieg 1982). The extant species belong to the Neotanaidomorpha, the Tanaidomorpha, and to the super family Apseudoidea, which is part of the suborder Apseudomorpha. These suborders contain 18 families representing approximately 600 described species. No definitive work on the Tanaidacea of the Gulf of Mexico is presently available and records are limited to only a few published works. The purpose of this series of publications is to produce much new information on the zoogeography, taxonomy, systematics and ecology of the Tanaidacea occurring in the Gulf of Mexico.

ACKNOWLEDGMENTS

We thank Lucia O'Toole for typing the manuscript.

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Gulf Research Reports

Volume 7 | Issue 2

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DOI: 10.18785/grr.0702.02

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Sieg, J., R. W. Heard and J. T. Ogle. 1982. Tanaidacea (Crustacea: Peracardia) of the Gulf of Mexico. II. The Occurrence of *Halmyrapseudes bahamensis* Băcescu and Gutu, 1974 (Apseudidae) in the Eastern Gulf with Redescription and Ecological Notes. Gulf Research Reports 7 (2): 105-113.

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TANAIDACEA (CRUSTACEA: PERACARIDA) OF THE GULF OF MEXICO. II. THE OCCURRENCE OF *HALMYRAPSEUDES BAHAMENSIS* BĂCESCU AND GUȚU, 1974 (APSEUDIDAE) IN THE EASTERN GULF WITH REDESCRIPTION AND ECOLOGICAL NOTES.

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ABSTRACT *Halmyrapseudes bahamensis* Băcescu and Guțu, 1974 is reported from two localities in the northeastern Gulf of Mexico. A redescription is presented based on examination of type material and a large collection of Gulf specimens. Ecological notes are presented on the occurrence, seasonality and distribution of *H. bahamensis* in two tidal marsh systems near St. Marks, Florida. The taxonomic status of *H. bahamensis* in relation to the two other described species of *Halmyrapseudes* is discussed.

INTRODUCTION

Subrahmanyam, Kruczynski and Drake (1976) reported "*Apseudes* sp." from tidal marshes near St. Marks, Florida. They suggested that their specimens might be "*Apseudes alicii* King." However Ogle (1977) examined the specimens of "*A. alicii*" deposited in the National Museum of Natural History (USNM) and found them to belong to the genus *Kalliapseudes* Stebbing, 1910 noting that "*A. alicii*" is a *nomum nudum* having no published description. The senior author has examined the specimens of Subrahmanyam et al. (1976) and found them to be *Halmyrapseudes bahamensis* Băcescu and Guțu, 1974, a species originally described from Andros Island, Bahamas. Tanaidacean specimens collected at Naples, Florida, which are now in the collection of the National Museum of Natural History (USNM), Washington, D.C., have also proved to be this species. Based on the St. Marks and Naples specimens and type material, this report presents a supplemental and partial redescription of *H. bahamensis* and information on its ecology in two northeastern Gulf tidal marsh systems.

MATERIALS AND METHODS

With the exception of the Naples, Florida, material, specimens were collected during random monthly sampling at low tide from 1972 to 1974 in both zones "high" and "low" of marshes at St. Marks and Wakulla Beach, Florida, (see Coultas 1969, 1970). Emergent vegetation was cut to ground level and a 0.0625 m² sample of marsh substrata 10 cm deep was taken. Salinity, water temperature and depth were measured at the time samples were collected. Samples were taken to the laboratory and washed through a series of sieves, 1 mm being the smallest. The organisms obtained were preserved in 10% formalin, stained with rose

bengal and sorted under a dissecting microscope. Methods used for the collection of the Naples, Florida specimens are at present unavailable. Type material from the USNM and Muséum d'Histoire Naturelle "Grigore Antipa" was examined by the senior author.

Halmyrapseudes bahamensis Băcescu and Guțu, 1974

Halmyrapseudes bahamensis: Băcescu and Guțu, 1974: 96–100; Băcescu and Guțu, 1975:111; Heard, 1982: 30.

Apseudes sp.: Subrahmanyam, Kruczynski and Drake, 1976: 174, 179, 181, 184, 185, 190–192.

Material Examined — Andros Island, Bahamas, 1970, 2 ♂, 1 ♀ (2 ♂♂ USNM 171401), 1 ♀ Muséum d'Histoire Naturelle "Grigore Antipa" No. 249, Bucarest, Romania; St. Marks, Florida, 1972–1974, 94 ♀♀ + 95 ♂♂ (3 ♂♂ + 4 ♀♀ in Coll. J. Sieg; 4 ♀♀ + 3 ♂♂ in Coll. J. Ogle, 4 ♂♂ in Coll. R. Heard, remaining material in Coll. W. Kruczynski); Naples, Florida, 4 ♂♂, 6 ♀♀ (USNM 181929).

Description of female (Figs. 1–4).

Body — Length of the females about 4.2–4.5 mm; subadults and manca stages proportionately smaller; somewhat less than 6.3 times longer than broad (Fig. 1).

Cephalothorax — Gently rounded and with an indentation in the middle of each side; excluding rostrum as long as broad; rostrum triangulated and relatively well developed.

Peraeonites — All peraenites with 1 or 2 setae at the anterior and posterior corner; first peraenite three times broader than long, anterior and posterior border smoothly concave, also rounded laterally in dorsal view; second 2.5 times broader than long, rounded laterally in dorsal view; third about 1.9 times broader than long, becoming somewhat broader posteriorly; fourth and fifth of same size, equal to the third but 1.5 times broader than long; sixth

peraeonite of same dimensions as the first, but straightened anteriorly (Fig. 1).

Pleonites — Five tergites dorsally visible, all of same size, four times broader than long; with a row of plumose setae at the lateral margins, these rows on the first 3 segments also curved inwards to the middle of the tergite (Fig. 1).

Antenna 1 (Fig. 1) — Consisting of a four-jointed peduncle, a two-jointed inner flagellum and a six-jointed outer flagellum; first joint of peduncle 2.7 times longer than broad, outer margin with 3 setae at the middle and 3 distally, inner margin with 4 feathered hair setae proximally and 6 hair setae distally; second joint about 1.6 times longer than broad, outer margin with 2 setae proximally and 3 setae distally, inner margin with 1 seta at the middle and 3 setae as well as 2 feathered hair setae distally; third joint only somewhat longer than broad, with single distal seta at the inner and outer margin; fourth with a projection and 2 setae; first and second joint of inner flagellum 2.9 times longer than broad, first with 1 distal seta and second with 4 setae distally; first and second joint of inner flagellum as long as broad and inner margin with 1 or 2 setae distally; third to sixth joint 2.3 times longer than broad, third and fifth only with single seta distally and fourth with 3 setae distally; sixth with 1 aesthetasc, 3 short and 3 long setae.

Antenna 2 (Fig. 1) — Consisting of a two-jointed peduncle, a squama, and an eight-jointed flagellum; first joint of peduncle with a strong and broad projection bearing 4 setae, second only somewhat longer than broad, outer margin with 1 seta distally, inner margin with a seta near the articulation of squama, this three times longer than broad with 3 setae distally; first joint of flagellum only little longer than broad and outer margin with 5 setae distally; second 1.5 times longer than broad, outer margin with 1 feathered hair seta and 1 seta in the middle and inner margin with a row of 4 setae; third 1.7 times longer than broad, outer margin with a row of 4 setae and a feathered hair seta, inner margin with 2 setae and 1 feathered hair seta; fourth to eighth joint small, only somewhat more than two times longer than broad, fourth, sixth and seventh joint each with 1 seta at the inner and outer margin distally, fifth joint at the inner margin with 2 setae and at the outer margin with 1 seta distally, eighth with 1 short and 4 longer setae.

Labrum (Fig. 2) — Hood-like, nearly completely covered with fine hair setae.

Mandibles (Fig. 2) — Well developed, with a three-jointed palpus; first joint only somewhat longer than broad, inner margin with 3 setae; second 2.7 times longer than broad, inner margin with 2 rows of 6 or 7 setae and outer margin with 1 seta at the middle; third joint 1.6 times longer than broad with 9 setae distally; corpus of mandibles strong, left mandible with lacinia mobilis and right without, spiniferous lobe with 8 small spines, pars molaris also strong.

Labium (Fig. 2) — Consists of only 1 lobe which is deeply divided in the middle, with a large terminal lobe which

bears 2 two-pointed spines and is completely covered with fine hair setae.

Maxilla 1 (Fig. 2) — Consists of an inner and outer endite as well as a two-jointed (?) palpus bearing 2 long and 3 short setae; inner endite with a projection at the outer margin and with 4 distal spines; outer endite with 10 strong spines.

Maxilla 2 (Fig. 2) — Outer margin with some serrations and set with fine hair setae; inner margin set with fine hair setae along the distal half; rostral row of the outer end consists of about 14 setae and caudal row of fixed endite with 1 caudal subterminal spine, distally with 5 normal spines, 1 plumose setae and 4 forked spines; outer lobe of the movable endite bears 3 long setae with single row of hair setae along the distal part and 1 normal seta.

Maxilliped (Fig. 2) — Coxa short, without setae; caudal surface of basis with 6 long setae distally near the articulation of palpus; palpus four-jointed; first joint as long as broad, with 1 distal spine at the outer margin; second nearly 1.2 times longer than broad, inner margin with a rostral and caudal row of 11 setae, outer margin with 1 spine distally; third only somewhat longer than broad, inner margin with a caudal and rostral row of 6 setae; fourth joint 1.8 times longer than broad, with 8 setae; each endite with 3 couplers and 1 long and 1 shorter caudal seta, inner margin with a row of 11 setae with double row of hair setae; distal margin with 11 normal setae.

Eipnath (Fig. 3) — Set with fine hairs and in front furnished with two melted oval lobes; terminal membranous spine covered with some fine hairs.

Cheliped (Fig. 4) — Coxa very small, bare; basis 1.6 times longer than carpus, with a broad projection distally, with 5 setae mid-rostrally, 2 sternal setae more proximally, a group of 5 setae mid-sternally and also 4 distal setae sternally; exopodite slender, three-jointed, last joint with 4 plumose setae; merus with 5 setae proximally and 6 setae distally; carpus slender, three times longer than broad, with a rostral and caudal row of setae tergally and at the sternal margin with 6 setae; propodus and fixed finger two times longer than broad, with some tergal setae rostrally and caudally, with 1 seta rostrally and 5 setae and 1 feathered hair caudally near the articulation of dactylus, fixed finger with 4 setae sternally, a spine at its tip and there 3 small setae, tergal margin with 9 small plumose setae; dactylus with spine and 3 setae tergally.

Peraeopod 1 (Fig. 3) — Fossorial; coxa without any projection; basis two times longer than broad, exopodite three-jointed and last joint with 5 plumose setae, with 2 rostral setae sternally and a row of 8 setae tergally, also 2 spines and a group of 5 setae distally; ischium small and with a group of 4 distal setae tergally; merus strong and flattened, mid-tergally with a row of 6 rostral setae, sternal margin with 4 setae and a distal spine, distal end of tergal margin with a strong spine and 6 setae; carpus somewhat shorter than merus, sternal margin with a row of about 16 rostral

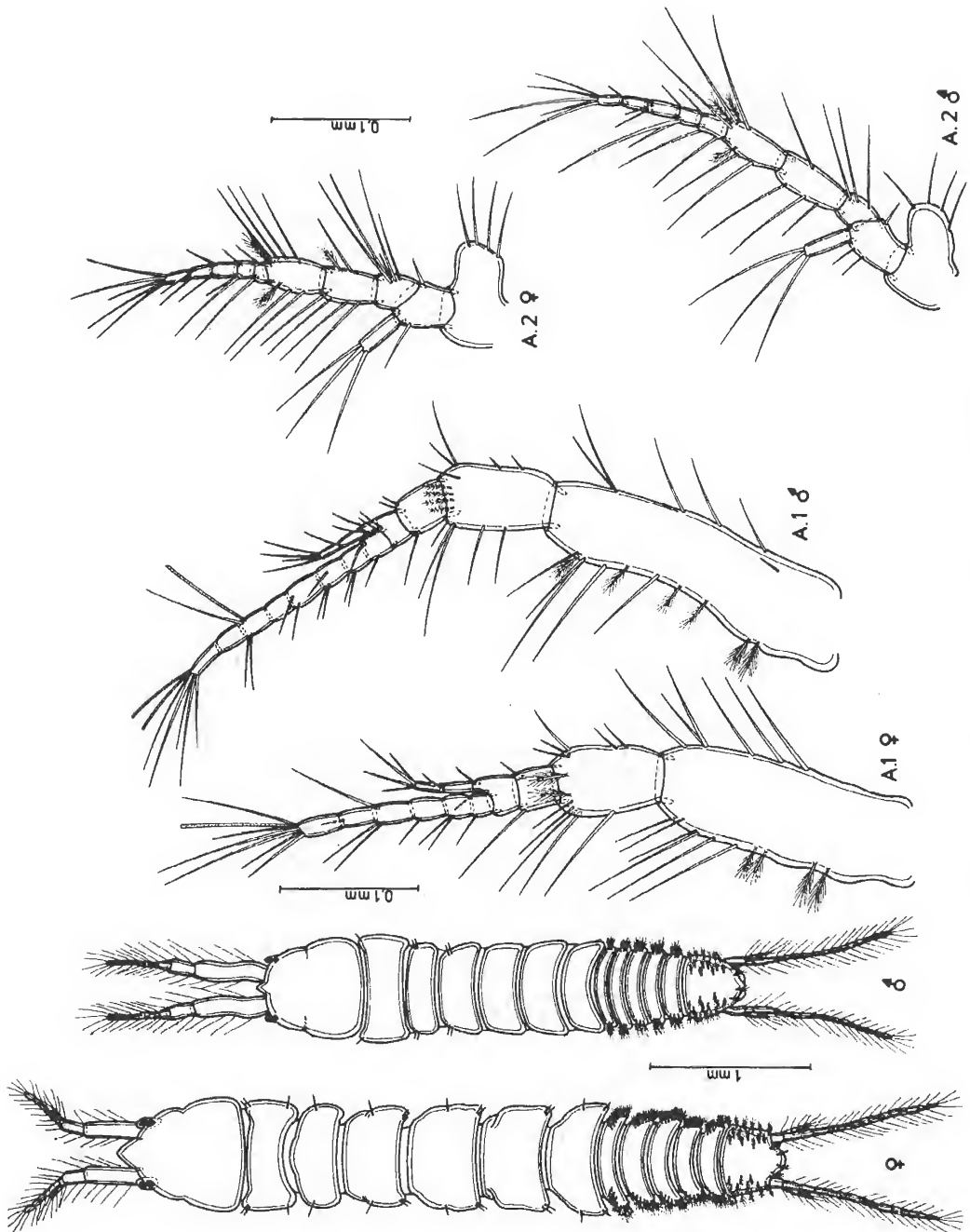


Figure 1. *H. bahamensis*; male and female, dorsal; A1 = Antenna 1; A2 = Antenna 2.

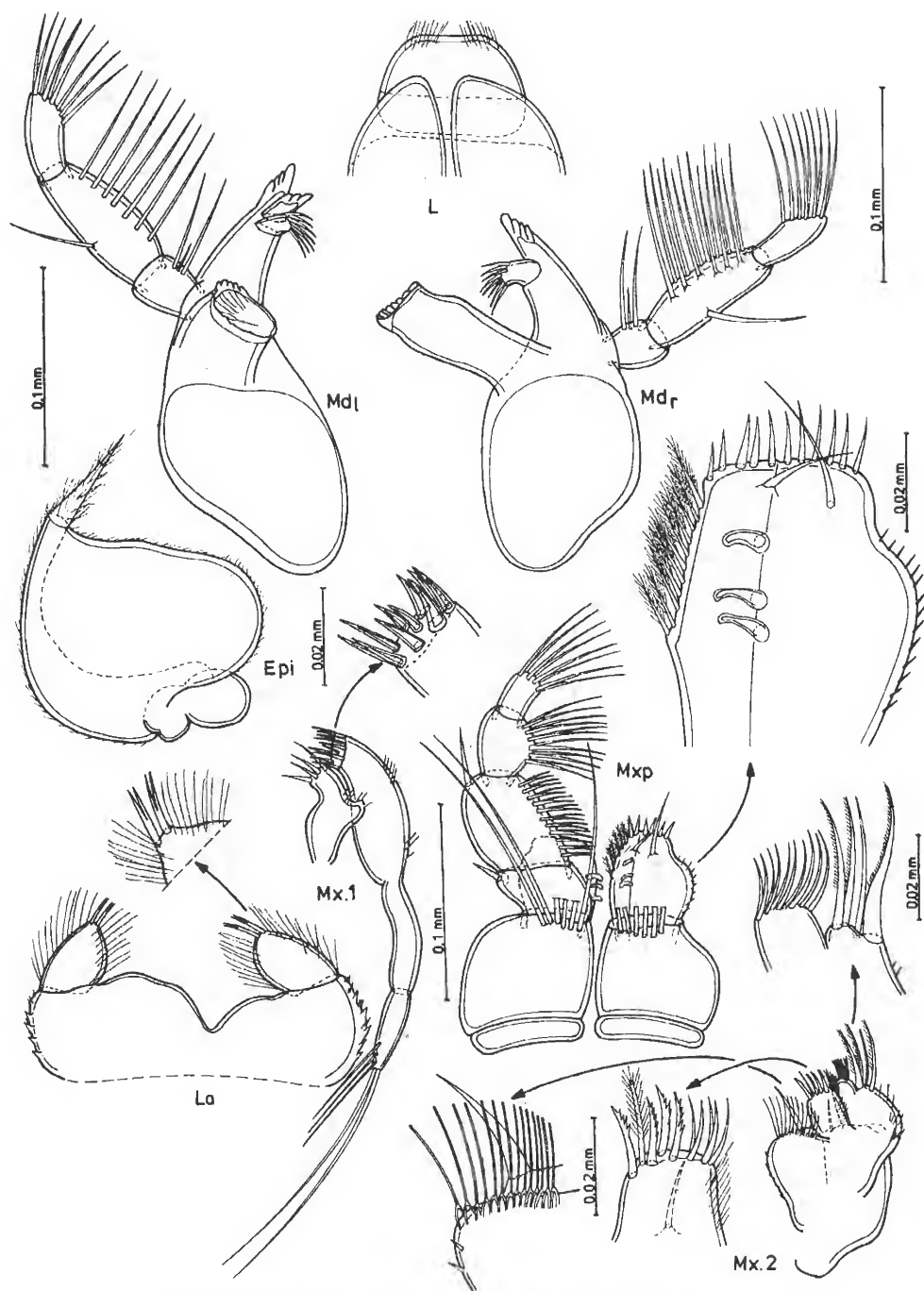


Figure 2. *H. bahamensis*; female; L = labrum; Md_l = left mandible; Md_r = right mandible; La = labium; Mx.1 = Maxilla 1; Mx.2 = Maxilla 2; Mxp = Maxilliped; Epi = Epignath.

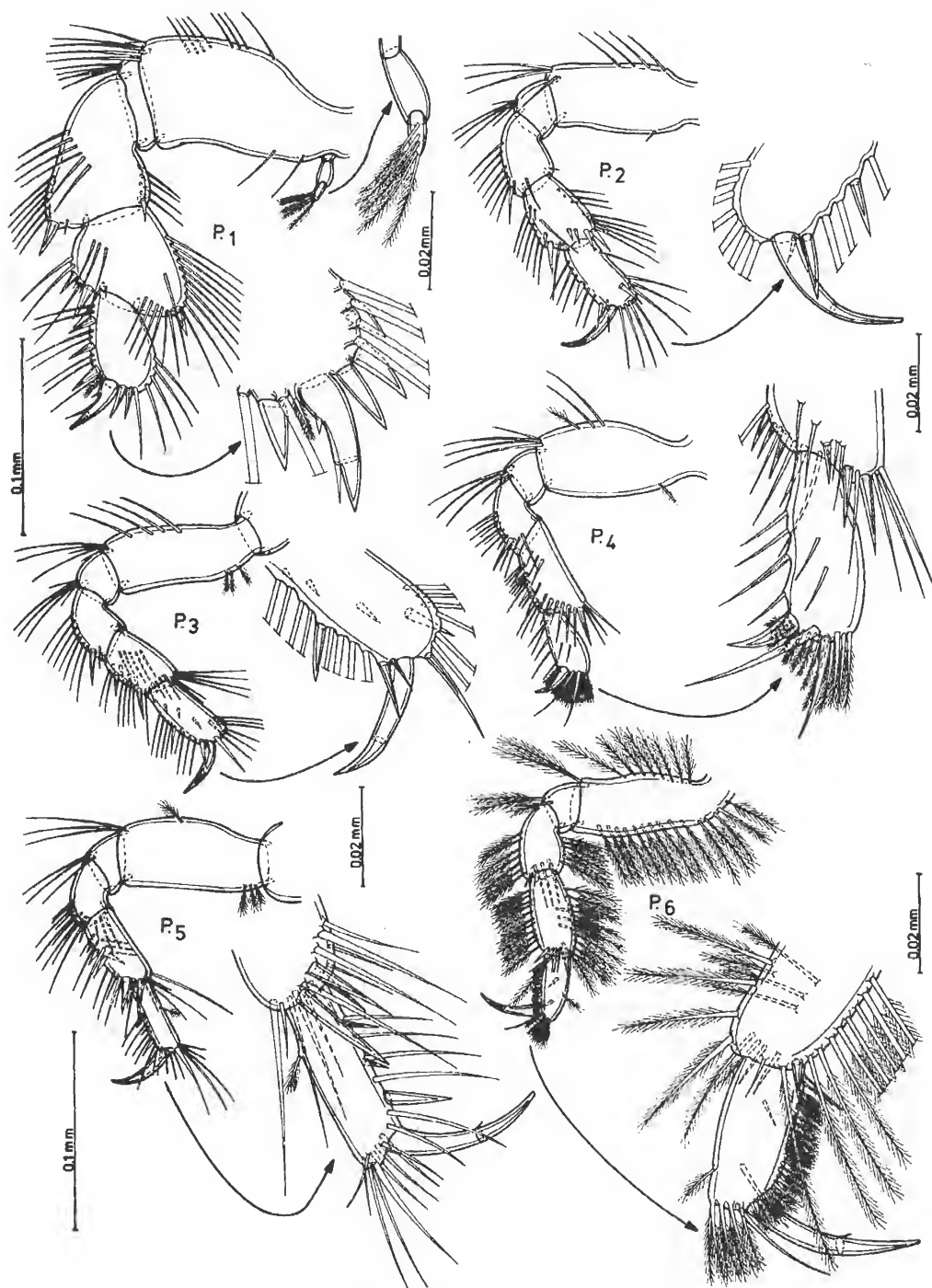


Figure 3. *H. bahamensis*; female; P 1-6 = pereopod 1-6.

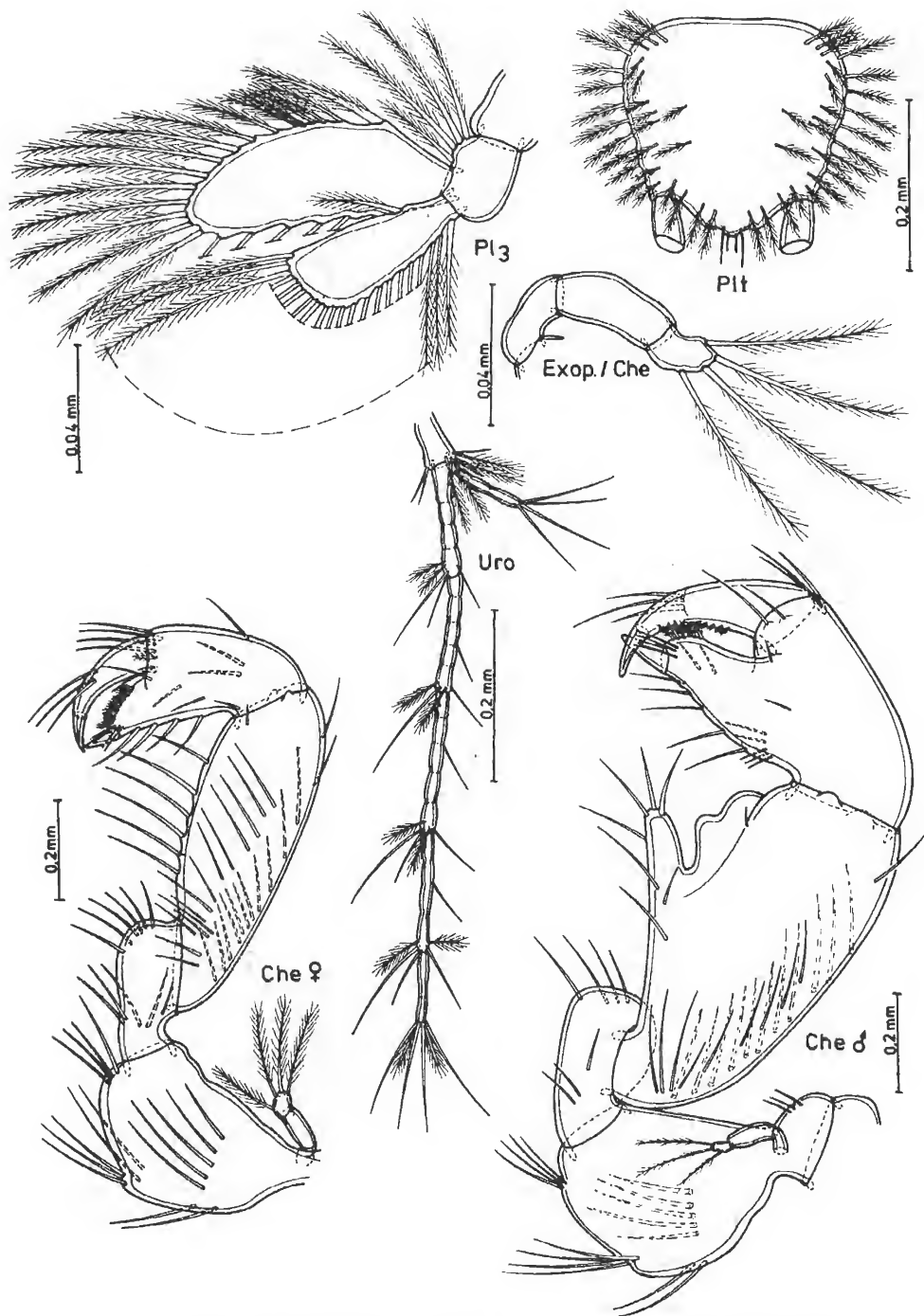


Figure 4. *H. bahamensis*; male and female; Che = cheliped; Pl_3 = third pleopod (female); Plt = pleotelson (female); Uro = uropod (female); Exop/Che = exopodite of cheliped.

setae, a caudal spine distally, mid-rostrally with 3 setae, tergal margin with 2 spines, 4 longer setae and 1 short seta; propodus smaller, as long as carpus, sternal margin with 5 rostral setae and with 2 rostral spines distally, tergal margin with alternating 2 setae and a strong spine, with a feathered hair distally; dactylus with a short spine and 2 spiniform projections.

Peraeopod 2 (Fig. 3) — Smaller than *P. 1*; basis 2.5 times longer than broad, with 1 seta sternally, with 4 rostral setae mid-tergally, and 4 distal setae; ischium as long as broad, with 3 long and 2 short distal setae; merus 1.4 times longer than broad, with 1 small distal seta sternally, with a row of 7 tergal setae, 2 small and 1 long spine; carpus 1.5 times longer than broad, sternal row consists of 8 caudal setae, also 4 distal spines sternally, tergal row consisting of 7 setae, also 2 small proximal spines and 1 small and 1 large spine distally; propodus 2 times longer than broad, tergal with 1 proximal seta and 7 setae as well as 1 spine distally, tergal margin with 6 setae and 2 spines; dactylus with spine, together nearly as long as propodus.

Peraeopod 3 (Fig. 3) — Similar in proportions and armament to *P. 2*; only propodus bears 3 distal spines instead of two.

Peraeopod 4 (Fig. 3) — Basis 2.2 times longer than broad, sternal with 1 proximal hair rostrally, tergal with 2 setae and 1 feathered hair mid-rostrally and 4 setae distally; ischium as long as broad with a group of 4 distal setae; merus 1.5 times longer than broad, slanted sternally, with a caudal row of 4 setae and 1 small spine as well as a rostral row of 6 setae and a long spine; carpus nearly 2 times longer than broad, rostral row beginning proximally and ending at the distal part of sternal margin consists of 11 setae and 3 spines, caudal row consists of 8 setae and 2 small spines; propodus 2 times longer than broad, tergal margin with 4 setae, distal part with a row of 14 two-sidedly ciliate setae and 2 long rostral setae; dactylus and spine seem to be coalesced to a claw.

Peraeopod 5 (Fig. 3) — Proportions as in *P. 4*; armament of basis, ischium, merus, and carpus as in *P. 4* only spines are somewhat stronger; propodus with a rostral feathered hair mid-sternally, tergal margin with 6 setae and 1 spine rostrally and 2 small setae, 1 spiniform; dactylus and spine not coalesced to a claw, together shorter than propodus.

Peraeopod 6 (Fig. 3) — Proportions as in *P. 4*/*P. 5* but armament different, all setae bear double rows of fine setae; tergal margin of basis with a row of 15 setae and sternal with 8 setae and additionally with 2 distal setae; ischium with 3 distal setae; merus with 6 sternal, 7 tergal, and 3 distal setae and a small distal spine; carpus with 13 sternal, 11 tergal, 2 distal setae as well as 4 short spines; propodus two times longer than broad, with a rostral feathered hair mid-sternally, with 7 short and 1 long setae distally, tergal margin with a proximal spine and a row of

about 22 small plumose setae, with a caudal spine proximally and distally.

Pleopods (Fig. 4) — All five pairs of pleopods are very similar; coxa fused with the sternite; basis about 1.5 times longer than broad only inner margin with 4 plumose setae; exopodite one-jointed, broad, margins covered totally with plumose setae, additional inner margin with 1 strong plumose setae proximally; endopodite also one-jointed and broad, only outer margin covered with plumose setae of which the most distal one is different—stronger and irregular ciliate—inner margin only with a proximal plumose seta.

Pleotelson (Fig. 4) — As long as broad, trapeziform; lateral and caudal margins covered with many plumose setae; caudal margin slightly alternated with 2 longer tergal and 2 smaller sternal setae.

Uropods (Fig. 4) — Consisting of basis, four-jointed endopodite and exopodite of about 20 "joints" forming five functional "segments"; inner margin of basis with 2 normal and 4 plumose setae distally, outer margin only with 2 normal setae distally; first to third joint of endopodite small, without setae, fourth joint about 2.5 times longer than broad with 4 distal setae; first "segment" of exopodite consists most times of 4 "joints," only the last one bears 2 feathered hairs and 3 setae distally; second "segment" consisting of 5 "joints," third bearing 1 distal seta and fifth with 2 feathered hairs and 2 setae distally; third "segment" consists also of 5 "joints," 3 setae distally; fourth "segment" with 4 "joints," second with 1 seta and fourth with 3 setae and 2 feathered hairs distally; fifth "segment" two-"jointed" with 2 feathered hairs and 4 setae distally.

Description of male (Figs. 1 & 4)

Body — Smaller than the female, about 3.5–3.6 mm, 5 times longer than broad (Fig. 1).

Cephalothorax — As in the female, only rostrum somewhat smaller.

Peraeonites — First and second similar to that of the females, but proportionately smaller; third to fifth peraeonite 2.5 times longer than broad, rounded laterally in dorsal view; sixth of same dimensions as second.

Pleon — Proportionately smaller as those in the females; about 5.4 times broader than long.

Antenna 1 (Fig. 1) — Consisting of a four-jointed peduncle, two-jointed inner flagellum and eight-jointed outer flagellum; armament of joints of peduncle very similar to those in the females; first joint about 4.1 times; second 1.6 times; third 1.3 times longer than broad; and fourth as long as broad; inner flagellum as in the females; first to seventh joint about 1.3 times longer than broad; first and second with 2; third with 3; and fourth again with 2 setae distally; fifth and seventh without seta; sixth with 1 aesthetasc and 3 setae distally; last joint about three times longer than broad with 2 aesthetascs and 5 setae distally.

Antenna 2 (Fig. 1) — Armament very similar to that of females but all joints somewhat longer.

Mouthparts — As in the females.

Cheliped (Fig. 4) — Much stronger than in the females; basis about 1.2 times larger than in the female sex, armament similar, exopodite also three-jointed, but last joint with 3 plumose setae; merus similar in armament and proportion to that of females; sternal margin of carpus at the middle with a strong small and flattened projection, this with 3 proximal and 4 distal setae, with 2 broad but shorter projections more distal and these without setae; propodus with fixed finger and dactylus with spine about 1.5 times larger than in the females, but armament very similar.

Peraeopods, pleopods, pleotelson and uropods — Very similar to those of the female sex.

Remarks — We observed minor variations in the small setae and spines on the peraeopods; the number of "joints" of "segments" in uropods seem to be variable but not the number of "segments." Sexual dimorphism is pronounced. The sexes have different body shapes (Fig. 1) with the males having a greater number of joints in the outer flagellum of antenna 1 and a much stronger cheliped with a carpus bearing large projections at the sternal margin.

Distribution (Fig. 5)

This species is known from its type locality, Bahama Islands, Andros Island muddy tidal flats on northwest side in tubes (male type USNM 153850, paratype USNM 153940). From Naples, Florida, 4 ♂♂, 6 ♀♀ (USNM 18129) and in extensive collections of Kruczynski from St. Mark and Wakulla Beach, Florida.

Taxonomy

This detailed redescription of *H. bahamensis* should aid in further distinguishing it from the other two named species of *Halmyrapseudes* Băcescu and Guțu, 1974, especially if only female specimens are available for study. Distinctive characters may occur in the mouth parts and in the armament of the peraeopods, particularly in their spination. *Halmyrapseudes bahamensis* is similar to the other two described species of the genus, *H. cubanensis* Băcescu and Guțu, 1974 and *H. spaansi* Băcescu and Guțu, 1975. *Halmyrapseudes cubanensis* and *H. spaansi* are both presently known only from their type localities in Cuba and Surinam, respectively. At present the three species can only be reliably separated from each other by the described morphological differences in the chelae of the adult males; therefore, a revision of the species of *Halmyrapseudes* with a detailed comparison of the females is needed to further clarify their systematic and taxonomic status.

Ecological Notes

The ecology of two tidal marshes, St. Marks and Wakulla Beach, from which most specimens of *H. bahamensis* were

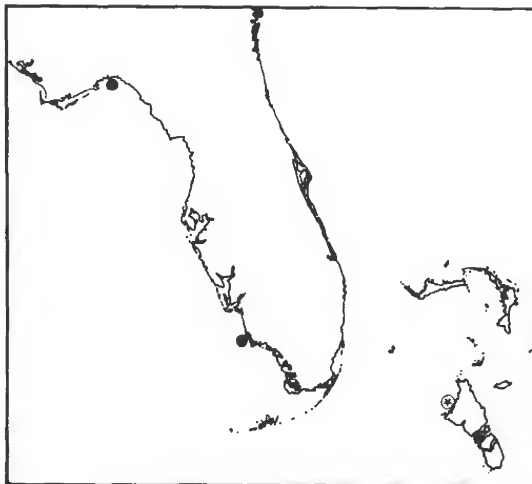


Figure 5. Known distribution of *H. bahamensis*. Circled star represents type locality; black dots represent the new Gulf of Mexico localities.

collected, has been described in detail by Subrahmanyam and Drake (1975); Subrahmanyam, Kruczynski and Drake (1976); and Kruczynski, Subrahmanyam and Drake (1978). Both areas are undisturbed marshes with almost pure stands of *Juncus roemerianus* from the waters edge to approximately 500 m inland. Coultas (1969, 1970) studied soil characteristics of these marshes and divided them into low and upper areas based on sediment characteristics.

Temperature at the St. Marks-Wakulla Beach tidal marsh sites varied from 11° to 35°C and salinity varied from 10 to 30 ‰ during the sampling period. Mean water depth at high tide was 19.5 cm for low marsh and 9.5 cm for upper marsh areas at both marshes. Abundance of *H. bahamensis* and another tanaid, the paratanaid *Hargeria rapax* (Harger 1879) is summarized in Table 1. *Halmyrapseudes* was more numerous than *H. rapax* (Harger 1879) in the low marsh zone of both marshes. *Hargeria* was more numerous than *Halmyrapseudes* in the upper zone at St. Marks, whereas, *Halmyrapseudes* was more abundant than *Hargeria* in the upper zone at Wakulla Beach. Both species of tanaidaceans were most abundant between January 1973 and April 1973 and December 1973 and May 1974. During these colder periods of the year, the marsh substrata is damper and generally more oxygenated than during the hotter late spring, summer and early fall periods. These conditions probably have a major effect on the seasonal fluctuations in the two tanaid populations.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to Dr. William Kruczynski, formerly with Florida A&M University's saline

TABLE 1.

Abundance of tanaidaceans in .0625 m samples taken monthly in two *Juncus roemerianus* marshes in northwestern Florida, U.S.A.

St. Marks Marsh					Wakulla Beach Marsh				
Date	Low Marsh		Upper Marsh		Date	Low Marsh		Upper Marsh	
	Halmyrapseudes	Hargeria	Halmyrapseudes	Hargeria		Halmyrapseudes	Hargeria	Halmyrapseudes	Hargeria
10 Aug 72	0	0	0	1	15 Aug 72	0	0	0	0
14 Aug 72	0	0	0	0	16 Aug 72	0	10	0	3
21 Aug 72	0	0	0	0	30 Aug 72	0	0	0	0
30 Sep 72	0	0	0	0	2 Sep 72	0	0	0	0
19 Oct 72	0	0	0	0	5 Oct 72	0	0	0	0
16 Nov 72	0	0	0	0	2 Nov 72	0	0	0	0
					18 Nov 72	0	0	0	0
27 Jan 73	1	2	0	10	1 Feb 73	6	1	0	0
1 Mar 73	89	45	1	4	4 Mar 73	5	0	33	0
15 Mar 73	22	1	0	1	18 Mar 73	10	4	0	0
21 Apr 73	10	3	1	5	22 Apr 73	25	6	1	0
20 May 73	0	0	0	0	24 May 73	1	0	0	0
15 Jun 73	0	0	1	6	14 Jun 73	0	0	0	0
7 Jul 73	0	0	0	1	9 Jul 73	1	0	0	0
6 Aug 73	0	0	0	0	7 Aug 73	1	1	0	0
4 Sep 73	3	0	0	2	5 Sep 73	0	0	0	0
2 Oct 73	0	2	0	9	4 Oct 73	0	0	7	0
5 Nov 73	0	0	0	0	6 Nov 73	7	0	0	0
4 Dec 73	28	0	1	7	6 Dec 73	0	5	0	0
14 Jan 74	1	0	0	0	12 Jan 74	1	0	0	0
24 Feb 74	3	0	0	2	27 Feb 74	6	0	0	19
23 Mar 74	11	0	0	1	25 Mar 74	0	1	0	0
25 Apr 74	7	1	0	0	28 Apr 74	3	1	1	2
30 May 74	13	1	0	0	25 May 74	0	0	0	0
20 Jun 74	0	9	0	4	21 Jun 74	0	0	0	0
23 Jul 74	21	1	0	0	26 Jul 74	0	0	0	0
12 Aug 74	0	0	0	0	13 Aug 74	0	0	0	0
TOTALS	209	65	4	53		66	29	42	24

marsh project, for providing ecological data and specimens from the St. Marks-Wakulla Beach salt marshes. Charles

Messing made available the specimens from Naples, Florida, and Sharon Wilson typed the manuscript.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.03

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SPATIAL AND TEMPORAL PATTERNS IN THE MACROBENTHOS OF ST. LOUIS BAY, MISSISSIPPI

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ABSTRACT Benthic community structure in St. Louis Bay was studied for 23 months. Cluster analyses distinguished two habitats: open water areas and areas near the marshy shores of rivers and bayous. Two groups of "euryhaline opportunistic" species were dominant at the open water stations. Temporal patterns of the "euryhaline opportunists," which appeared to be controlled by a combination of reproductive pulses and seasonally intense predation, showed that the greatest abundance of macroinfauna occurred during the cooler months with reduced recruitment during the second year. The river-bayou stations were characterized by two groups of "estuarine endemic" species. One of these groups was most abundant in the warmer months and the other in the cooler months. Changes in abundance of the "estuarine endemics" appeared to reflect seasonal cycles.

INTRODUCTION

Early quantitative investigations of benthic macroinfauna were generally concerned with trophic relationships (Petersen 1918). In addition to food web considerations, recent studies have been concerned with the use of benthic macroinvertebrates as biological indicators of water quality and environmental perturbation because of their relative immobility, long life, sedentary habits, and differing tolerance to stress (Copeland and Bechtel 1971, Young 1974). The importance of benthic communities in the ecological description of coastal areas is now well understood, as witnessed by the vast number of environmental impact statements that include benthic studies. If a benthic study is to be more than just a list of fauna collected, it must also describe the distribution and abundance of the species in time and space.

Boesch et al. (1976) pointed out that detailed knowledge of long-term regional community dynamics is necessary to interpret site-specific surveys and that without such knowledge natural variation may be mistaken for the effect of a pollutant, or worse, vice-versa. A few benthic studies have been conducted in the St. Louis Bay, Mississippi, area (Christmas and Langley 1973, Guy 1973, Water and Air Research Inc. 1975, Milligan 1979) but in each case their design, duration or intensity limited their usefulness in providing information about temporal or spatial variation of the benthos. The present effort, a 23-month study of the benthos of St. Louis Bay, was designed to contribute to the knowledge of natural fluctuations of the bottom communities of a low salinity area of Mississippi Sound.

Area description

St. Louis Bay is a mushroom-shaped extension of the western portion of Mississippi Sound (Figure 1). The bay is approximately 10 km wide and 7.3 km long. The mouth is 2.8 km wide. Tides in the area are diurnal with a mean range

of approximately 0.5 m. The bay receives fresh water from the Jourdan River on the west and the Wolf River on the east. The northern shores of the bay are fringed by *Juncus-Spartina* marshes. The eastern and western shores are developed as residential property.

Samples were collected at 13 locations in St. Louis Bay (Figure 1) at approximately monthly intervals from December 1977 through October 1979. Stations 1, 3, 5, 9, 11, 17, 18, and 19 were located in open water at depths of 1 to 2 m. Stations 6 and 21 were located about 1 m from the marsh banks of the Jourdan and Wolf Rivers, respectively. Station 22 was also near the marshy shore of Bayou Portage. The substratum at all these stations was sandy mud with considerable organic detritus and the depth was generally less than 2 m. Station 15 was located near the navigation channel in 2.5 to 3.5 m of water. The substratum was very soft grey mud. Station 24 was located on a subtidal sandbar in 1 to 1.5 m of water.

MATERIALS AND METHODS

Benthic infauna was sampled with a 0.023-m² Ekman grab. The grab was mounted on a long handle so that depth of penetration (11 to 15 cm) could be controlled, regardless of sediment characteristics, by pushing it into the substratum. At each station, three grabs were collected for infauna and a fourth grab was collected and subsampled for total organic carbon and grain size analyses. *In situ* measurements of surface and bottom water temperature, salinity, and dissolved oxygen were made prior to each collection. Benthic samples were washed into nested sieves with openings of 2.0 and 0.5 mm. Organisms, along with shell fragments, plant debris, and other detritus remaining on the sieves, were preserved in 10% formalin and stained with rose bengal. Organisms were sorted under an illuminated magnifier and stored in 70% ethanol until they could be identified and counted. Faunal data from the three replicates at each collection, hereafter referred to as station-dates, were recorded separately but pooled for analysis. Total organic

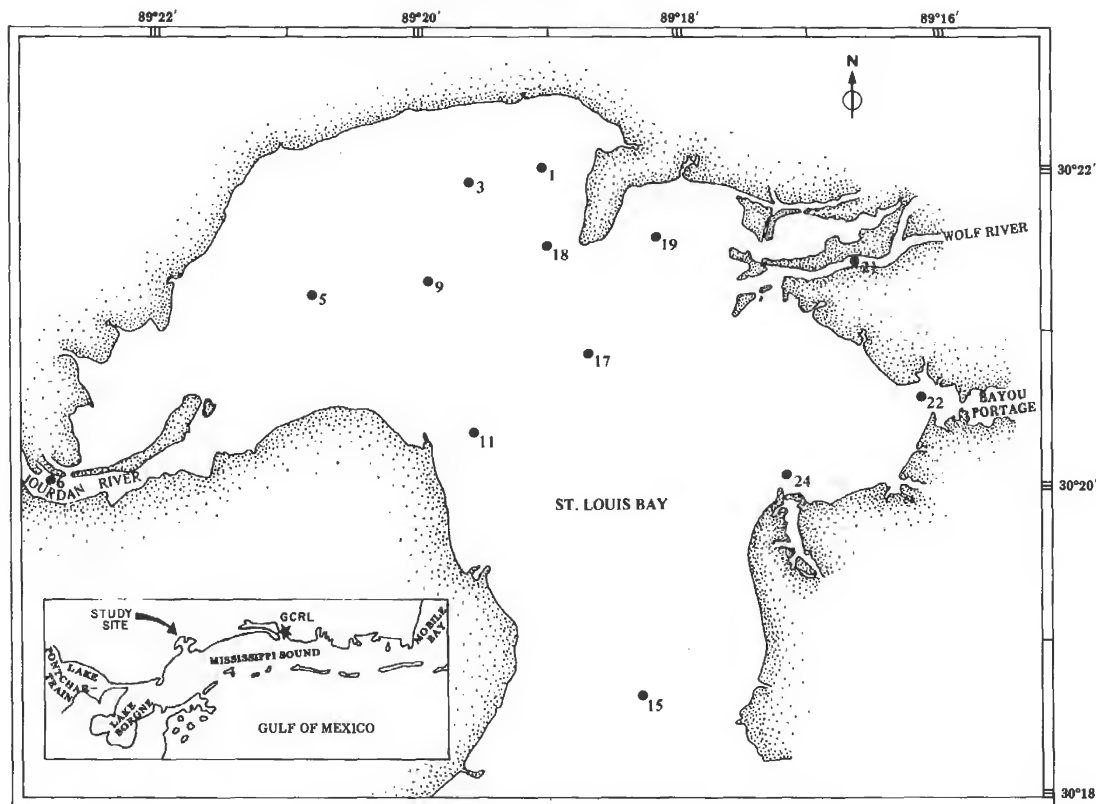


Figure 1. Map of station locations in St. Louis Bay.

carbon and sediment grain size analyses were performed by the Environmental Chemistry and Geology sections, respectively, of the Gulf Coast Research Laboratory (GCRL).

Faunal data were subjected to cluster analysis as a means of showing temporal, spatial, and species associations within St. Louis Bay. The objective of this type of analysis is to group either the entities (station-dates) or the attributes (species) into clusters such that elements within a cluster have a high degree of "natural association" among themselves and are "relatively distinct" from one another (Anderberg 1973). The Bray-Curtis coefficient of dissimilarity was used as the distance measure for these analyses. This coefficient, which is also known as the Czekanowski Quantitative Index (Bloom 1981), can be expressed as either a similarity or dissimilarity index. The dissimilarity form is:

$$D = \frac{\sum_j |X_{1j} - X_{2j}|}{\sum_j X_{1j} + X_{2j}}$$

where X_{1j} and X_{2j} are the values of the j th variable for the two entities or attributes being compared. In testing four common similarity indices against each other and a theoret-

ical distribution, Bloom (1981) found that only the Bray-Curtis index accurately reflected similarity.

The results of the Bray-Curtis comparisons were sorted using a flexible sorting strategy (Lance and Williams 1966, 1967) with the cluster intensity coefficient, β , set at the conventional value of -0.25 . This strategy is intensely clustering and moderately space dilating (Boesch 1977a). Because of a scale problem that exists with all metric coefficients and coefficients derived from metrics (Boesch 1973), a square root transformation was applied so that the largest numbers in the data set were reduced to numbers between 20 and 25 (Dr. William Stephenson, University of Queensland, personal communication). For the inverse analysis, each taxon was standardized by dividing the number of individuals in a collection by the total number of individuals in that taxon. Since very rare species contribute little or no new information to Bray-Curtis analysis, all species taken only three or fewer times during the study were eliminated from the data set prior to analysis. In addition, fish, barnacles, and *Membranipora* sp. were eliminated because of gear selectivity. No reallocation of entities or attributes was deemed necessary.

The cluster analyses were performed using the CLASS program developed by Dr. Robert Smith at the University of Southern California. In order to reduce the size of the data matrix to conform to the program limitations, stations 15 and 24 and the December 1977 samples were eliminated. These eliminations were based on the analysis of the first 13 months of data which showed stations 15 and 24 grouped together for the entire year, and December 1977 collections grouped with those from the first three months of 1978. The grouping of stations 15 and 24 appeared to be the result of their each having reduced numbers of species common to all stations and lacking a unique faunal group. They were, in fact, physically very dissimilar. It was also felt that since December 1977 collections were so tightly grouped with those from the first three months of 1978 they could be eliminated with very little loss of information. These same patterns were shown in the analyses of combined years for stations (summed over time) vs. species and months (summed over stations) vs. species.

Station-date and species groupings were based on the dendrogram and a two-way coincidence table containing the untransformed data. Constancy (in percent) for each species group was determined as the total number of times that the constituent species occurred within a particular station-date group divided by the maximum possible number of occurrences in that station-date group. Fidelity refers to the number of times a species group occurred in a given station-date group divided by the total number of occurrences for that species group.

RESULTS

Physical Parameters

Average bottom water temperatures in St. Louis Bay ranged from 6.4 to 31.2°C (Figure 2). The lowest temperatures during both years were encountered during December and January with the highest temperatures occurring in July and August. The general trends among years were very similar with observations never varying more than 4.5°C between the first and second year for any given month. Mean station temperatures for the 23-month period and the results of Duncan's new multiple range test (Table 1a) indicated little difference in temperature among stations.

Average bottom water salinities ranged from 0.3 to 15.8‰ over the 23-month period (Figure 2). Although the general trends were somewhat similar, the decrease in winter and spring bottom salinities appeared to be more extreme in 1979 than 1978 and the summer salinities showed a more drastic increase in 1978 than 1979. Average spring salinities appeared to remain lower for a longer period of time during 1979. Duncan's new multiple range test (Table 1b) indicated that the river stations (6 and 21) had significantly lower salinities ($\alpha = 0.05$) than other areas of the bay. The open water stations (1, 3, 5, 9, 11, 17, 18, and 19)

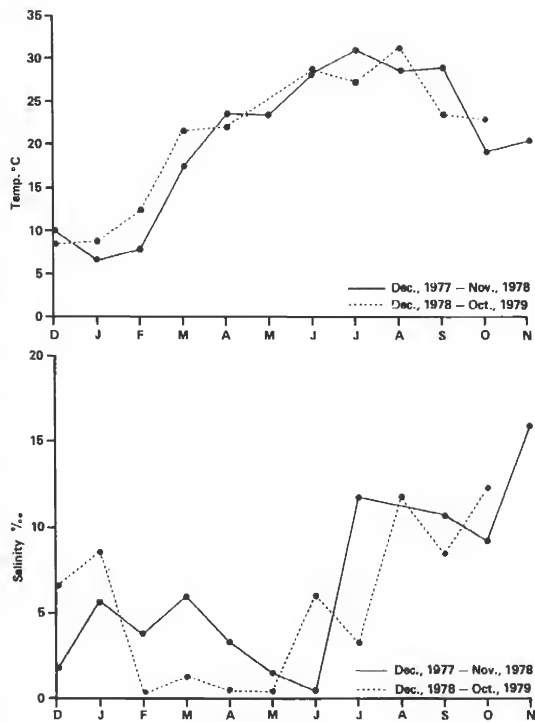


Figure 2. Average bottom water temperature and salinity in St. Louis Bay.

showed few significant differences with a high degree of overlap. Stations 15 and 24 had the highest average salinities and were significantly different ($\alpha = 0.05$) from each other and from other areas in the bay.

Differences between surface and bottom temperatures and salinities indicated no long term stratification of the water column. Dissolved oxygen only dropped below 4.5 ppm twice (stations 1 and 5, July 1978) and was not considered critical throughout the study.

Statistical analyses of the measured sediment parameters showed that only the percentage of clay was significantly different ($\alpha = 0.05$) among months. Mean values for each station and significant differences ($\alpha = 0.05$) among stations for each sediment parameter are shown in Table 1c-f. Even though the sediment parameters were correlated to each other, the analyses did not indicate consistent station groupings based upon all four parameters.

Fauna

A total of 79,382 individuals representing ten phyla was collected during 23 months of sampling. We identified 86 distinct taxa including 64 to genus or species level. Polychaetes were the most abundant taxonomic group, accounting for

TABLE 1.
Results of Duncan's new multiple range test showing significant differences ($\alpha = 0.05$) among stations
for temperature, salinity, total organic carbon, sand, silt and clay.

<hr/>													
a. Temperature °C													
Station	19	24	15	17	3	18	21	5	1	11	22	9	6
Mean Temp.	20.4	20.5	20.5	20.6	20.7	20.7	20.7	20.7	20.8	20.8	21.1	21.2	21.5
b. Salinity ‰													
Station	6	21	5	1	3	19	18	9	11	22	17	24	15
Mean Salinity	3.2	4.0	5.4	5.9	6.0	6.1	6.3	6.4	6.6	6.8	6.8	7.7	9.3
c. Total Organic Carbon %													
Station	24	22	17	18	1	11	19	3	9	5	21	15	6
Mean % TOC	0.6	1.0	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.8	1.9	2.1	2.6
d. Sand %													
Station	5	15	3	9	1	6	19	18	11	21	22	17	24
Mean % Sand	8.9	11.3	12.2	12.8	15.0	20.5	24.9	25.6	37.1	41.4	52.0	53.1	70.0
e. Silt %													
Station	24	17	11	15	22	21	18	19	3	5	9	6	1
Mean % Silt	15.1	22.5	34.8	35.9	36.3	40.2	40.9	42.5	45.7	49.0	50.1	51.5	53.1
f. Clay %													
Station	22	24	21	17	6	11	1	19	18	9	3	5	15
Mean % Clay	11.7	14.9	18.4	24.4	28.0	28.1	31.9	32.6	33.5	37.1	42.1	42.1	52.8
<hr/>													

47.9% of the total number of individuals. Mollusks were the next most abundant group (28.7%) followed by insects (9.3%) and crustaceans (8.1%).

Station groups

Flexible sorting of the station-dates indicated seven major groups (Table 2). Groups I and II are composed of collections from river stations (6 and 21) and the bayou station (22). The major difference between these two groups was the time which these stations grouped together. Group I generally represents the winter-early spring months of both years while group II is composed of collections from summer-fall months for these stations.

Groups III through VII are mainly composed of collections from the open water stations (1, 3, 5, 9, 11, 17, 18, and 19) with each group occurring during a specific time period (Table 2). During 1978 these stations formed three distinct groups: January-May (group III), June-July (group IV) and September-December (group V). Group IV also contained a few samples taken at the river stations (6 and 21) and bayou station (22) during the spring and summer of 1978. Group V also contains a majority of samples taken at the open water stations during June 1979. During 1979 the open water stations were in two time groups: January-March, September and October (group VI) and March, April, July, and August (group VII).

The dendrogram (Table 2) indicates the river stations (6 and 21) and the bayou station (22) (groups I and II) were

more similar to each other throughout the study period than they were to the open water stations (1, 3, 5, 9, 11, 17, 18, and 19). Collections taken at the open water stations during the first half of 1978 (groups III and IV) were more similar to each other and to the river and bayou stations than they were to the open water stations during the remainder of 1978 and all of 1979. Collections taken at the open water stations during 1979 (groups VI and VII) were more similar to each other than they were to group V (September-December 1978 and June 1979).

Species groups

Inverse analysis of 22 months of data yielded six species groups (Table 3). The species in group A represent the most abundant benthic organisms in St. Louis Bay (Table 4). Considering each year separately, the highest densities occurred during the winter and spring months at all stations (entity groups I, III, and VI). Recruitment of these organisms appeared to be much higher during the winter of 1978 than 1979. *Hobsonia florida*, *Streblospio benedicti*, and *Parandalia americana* were the only species in this group that had higher densities at the river and bayou stations during the winter and spring (entity group I) than at the open water stations for the same time period (entity groups III and VI).

The species of group B were most similar to those of group A (Table 3). They were more abundant and had higher constancies in the winter and spring months of each

TABLE 3.

Results of the inverse cluster analysis showing the composition and relative dissimilarity of the species groups.

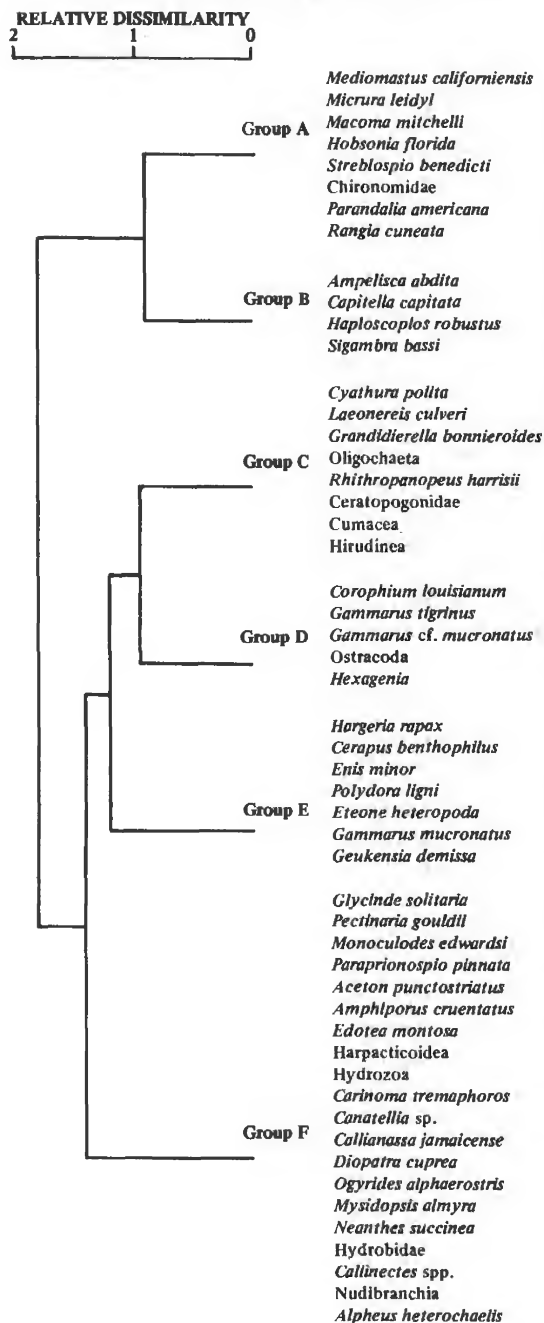


TABLE 4.

Summary table showing the mean constancy and mean number of individuals of each species group within each entity group.

	Entity Group I	Entity Group II	Entity Group III	Entity Group IV	Entity Group V	Entity Group VI	Entity Group VII
Species	95.65*	65.63	98.36	79.91	70.27	82.18	83.75
Group A	66.38†	15.36	59.42	37.92	7.21	21.42	10.12
Species	23.91	2.68	85.53	14.29	21.62	26.06	8.13
Group B	2.04	0.08	7.19	0.50	0.41	0.50	0.11
Species	44.57	59.82	2.96	9.38	2.70	7.18	2.19
Group C	8.83	15.22	0.06	1.55	0.09	0.27	0.04
Species	45.22	16.43	2.11	6.43	0.00	5.53	0.50
Group D	5.12	0.79	0.02	0.27	0.00	0.13	0.01
Species	25.47	7.65	3.38	1.53	0.77	9.12	1.43
Group E	1.85	0.30	0.05	0.02	0.01	0.29	0.01
Species	18.26	11.25	15.13	5.89	13.78	17.13	5.13
Group F	1.56	0.38	1.52	0.23	0.36	0.57	0.07

* Mean constancy in percent.

† Mean number of individuals of each species group within each entity group.

year than during the summer; however, the relative densities of these organisms were much lower than those of species group A for similar time periods (Table 4). The group B species were never very abundant at the river or bayou stations. Like the group A species, recruitment of group B species appeared to be greatly reduced during the winter of 1979.

Species groups C and D were most closely associated to each other and relatively dissimilar to groups A and B (Table 3). The species in these groups were most abundant and had the highest constancies at the river and bayou stations (6, 21, and 22) (Table 4). They had relatively low constancies and mean catches at the open water stations throughout the study period. Differences in these two species groups can be seen in the constancy and mean catch per cell at the river and bayou stations (entity groups I and II). The species in group C were relatively constant and had higher mean catches throughout the study period than the species in group D. Group D species were most abundant at the river and bayou stations during the winter and spring months (entity group I).

Species group E was most closely associated with the river and bayou stations, however, they were taken relatively infrequently. Species group F was loosely formed. These taxa were generally collected sporadically in relatively low numbers throughout the sampling period.

DISCUSSION

Spatial variation

Several investigators have demonstrated changes in benthic faunal assemblages based on gross changes from sand to mud sediments (Sanders 1958; Tenore 1972; Polgar 1975; Mountford et al. 1977; Whitlatch 1977; Loi and Wilson

1979; Maurer et al. 1979). However, Boesch (1973) found that most macrobenthic species in Hampton Roads, Virginia, were either not bottom-type specific or were restricted in varying degrees to sand bottoms. Except for station 24, all of the sample sites in this study averaged less than 54% sand, indicating mud or sandy mud sediments. The station-date dendrogram (Table 2) and the Duncan's multiple range test for sand (Table 1d) show no consistent pattern between the groupings of stations based on percent sand and the distribution of benthic infauna in St. Louis Bay.

Sanders (1958) also found that the distribution of dominant deposit feeders, the predominant trophic type represented in this study, correlated with percent clay composition of the mud sediments. Other investigators (McNulty et al. 1962, Santos and Simon 1974, Maurer et al. 1978) have shown the clay fraction to be relatively unimportant in influencing the distribution of deposit feeders. Station groupings in the station-date dendrogram (Table 2), determined mainly by the distribution of deposit feeders, show no relationship to those groups based on percentage of clay in the sediment (Table 1f).

Most estuarine organisms have a wide range of habitat selection. Sedimentary effects in estuaries are confounded with other environmental parameters such as depth, salinity, and seasonal changes (Tenore 1972). Boesch (1973), Watling (1975), and Whitlatch (1977) reported benthic faunal assemblages from the east coast which were ubiquitous within their respective study areas. In addition, Boesch (1973) also denoted a seasonally restricted species group. Two species groups in this study showed a similar distribution. Species group A contained the numerically dominant organisms and were taken consistently at all stations ($> 65\%$, Table 4). Species group B appeared to be seasonally restricted. They had the highest constancies during the winter and spring months (entity groups I, III, V, and VI).

Salinity is known to play an important role in the distribution of estuarine faunal assemblages. Tenore (1972) and Maurer et al. (1978) denoted a transition in benthic assemblages associated with a change from oligohaline ($< 5\text{‰}$) to mesohaline ($5\text{--}18\text{‰}$) waters in bays along the east coast. Boesch (1977b) stated that "euryhaline opportunistic" species decline in importance and number upestuary as their salinity tolerance limits are reached (approximately 5‰). "Estuarine endemic" species become more abundant below 5‰ .

The benthic faunal assemblages in St. Louis Bay exhibited a similar pattern. Species groups A and B were dominant throughout the sampling area. Salinities in open water portions of the bay conform to the range given by Boesch (1977b) for "euryhaline opportunists" and many of the species in these groups have been termed opportunistic by other investigators. Analysis of variance showed the river stations had significantly ($\alpha = 0.05$) lower salinities than the rest of the sampling area (Table 1b) with means $< 5\text{‰}$.

The species in groups C and D were faithful to these stations (87% and 76% fidelity, respectively). These species appear to be "estuarine endemic" and are important only in areas immediately adjacent to freshwater inflow. The bayou station (22) appeared to be transitional between the river and open water stations. It was located near an intermittent source of fresh water and the "estuarine endemic" species (groups C and D) were generally present when station 22 grouped with the river stations. The species in these two groups were uncommon during the periods when station 22 grouped with the open water stations.

Temporal changes

Various patterns of temporal variability in the benthos have been reported. In Delaware Bay, Watling (1975) reported repeating seasonal cycles with greatest infaunal density in June and the lowest in October. Lie and Evans (1973) found strong seasonal changes in Puget Sound, Washington; however, when compensated for seasonal variability they reported great year-to-year stability. Poore and Rainer (1979) found no seasonality in Port Phillip Bay, Australia, but rather strong aperiodic changes in the density of the common species and in the composition of the subdominant fauna. Along the temperate east coast of the United States, Tenore (1972), Boesch (1973), Holland et al. (1977), and Whitlatch (1977) have all reported seasonal changes in benthic infauna with greatest densities in the winter and spring. Benthic studies along the northern Gulf of Mexico coast by McBee and Brehm (1979), Johnson (1980), and Sikora et al. (1981) showed seasonal changes with the greatest density in the cooler months. Sikora et al. (1981) found repeating seasonal cycles; however, Johnson (1980) noted a continuous change in community structure throughout his study.

The nature of temporal changes of the benthic infauna in St. Louis Bay varied with habitat type. Seasonal changes at the river and bayou stations appeared to be cyclic. These stations clustered mainly in two groups: the cooler months of both years (group I), and the warmer months of both years (group II). Among the "estuarine endemic" species, group C was dominant throughout the study period. These species generally had seasonally comparable densities throughout both years with abundance peaks in the warmer months. Species groups D and E also had seasonally comparable densities during both years; however, they were only abundant during the cooler months.

The temporal variation at the open water stations was a result of fluctuations in abundance of the species in groups A and B. Species of these two groups, which had their highest constancy and abundance from January through May 1978 (group III), showed marked reductions in density during the warmer months (group IV). These reduced numbers continued through December 1978 (group V). The second year did not group, season-by-season, with the first year because of greatly reduced numbers of group A species

and the paucity of group B species. During 1979 the September and October samples from the open water stations grouped with the winter and spring months (group VI). This was apparently the result of an early fall recruitment with numbers approximating those of the delayed recruitment from the winter. The warmer months of 1979 generally formed a group (VII) which separated from 1978 because of greatly reduced numbers in the second year. This indicates that the open water stations may show cyclic changes in some years and aperiodic changes in others. Lack of uniformity such as this underscores the need for long term studies in any attempt to understand the dynamics of estuarine benthos.

Temporal changes in the benthos have been attributed to various causes. Seasonal spawning pulses were suggested by Tenore (1972), Boesch (1973), Holland et al. (1977), and Whitlatch (1977). Predation of adult or larval forms was thought to be important by Thorson (1966), Boesch (1973), Boesch et al. (1976), Virnstein (1977), and Cammen (1979). The depletion of benthic infauna in the summer months was linked to low dissolved oxygen concentrations by Tenore (1972), Holland et al. (1977), and Johnson (1980). Johnson also found changes in community structure related to drastic changes in salinity caused by a near-record flood following a prolonged drought. High mortality rates of newly set larvae caused by indiscriminant settling was mentioned by Cammen (1979) and Sikora et al. (1981).

There is undoubtedly a variety of mechanisms responsible for the temporal patterns observed in the St. Louis Bay infauna. The recruitment seen in the cooler months of both years was almost certainly caused by newly set juveniles because of the small size of the individuals. This is consistent with the seasonal spawning pulses observed along the temperate east coast of the United States.

Foraging by fishes is undoubtedly important to the fluctuations of the benthos of St. Louis Bay, particularly for the more abundant species (groups A and B). Darnell (1958) and Overstreet and Heard (1978) reported over 65% of the species in groups A and B from the stomachs of spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*). Cage studies have also indicated the importance of predation on benthic macroinvertebrates. Naqvi (1968) reported that the number of animals inside cages in Alligator Harbor, Florida, was four times the number in the surrounding substratum. Virnstein (1977) found that species populations in Chesapeake Bay were not resource limited but rather predator controlled. Trawl collections by the Fisheries Research and Development Section of GCRL (Dr. Thomas McIlwain, personal communication) showed that juvenile spot and croaker moved into St. Louis Bay in great numbers from May through July 1978 and April through July 1979. These months correspond to the times of reduced abundance of the species in groups A and B.

Dauer (1974) showed that in Tampa Bay, Florida, the

majority of benthic macroinvertebrates spawn more or less continuously. If summer spawning occurs in St. Louis Bay, predation on planktonic larvae may be an important factor. Boesch et al. (1976) discussed the impact of predation by the ctenophore *Mnemiopsis leidyi* on planktonic larvae of benthic macroinvertebrates. Unpublished data (Dr. Robert Woodmansee, GCRL, personal communication) show that *M. leidyi* was absent from the plankton during periods of greatest recruitment of group A benthic species and abundant during the months when recruitment was slight. The presence of this voracious planktivore could be important in limiting the success of recruitment during the warmer months. Thus, except possibly for extreme years, St. Louis Bay appears to exhibit physically controlled spatial patterns and biologically controlled temporal variability among the benthic macroinvertebrates.

Faunal comparisons

Comparison of the species taken in this study with those of similar studies along the Atlantic coast indicated that, except for lower Chesapeake Bay, few species were common to both areas. Boesch (1977b) reported 75 species from the York River area but only 16 of those were found in St. Louis Bay. In the Hampton Roads area, Boesch (1973) collected 168 species including 21 which were taken in this study. However, if only those species that were determined to be abundant enough to be used in the cluster analyses of each study were compared, the number of co-occurring species dropped to 13. Species groups defined by Boesch using cluster analysis for the York River and Hampton Roads areas were unlike the species groups of this study. Of the 74 species reported by Mountford et al. (1977) from the Calvert Cliffs area, 20 were found in St. Louis Bay. Comparing only the species that were considered abundant, only 8 were common to both areas. Based on these studies, 10 species (*Aceton punctostriatus*, *Cyathura polita*, *Ereone heteropoda*, *Glycinde solitaria*, *Monoculodes edwardsi*, *Neanthes succinea*, *Paraprionospio pinnata*, *Pectinaria gouldii*, *Polydora ligni*, and *Streblospio benedicti*) were abundant in the three areas of the lower Chesapeake Bay and St. Louis Bay. Other studies from the east coast (Tenore 1972, Polgar 1975, Watling 1975, Whitlatch 1977, and Cammen 1979) contained fewer than 8 species that were found in St. Louis Bay.

Benthic community studies in Gulf of Mexico estuaries indicated varying degrees of species similarity. Santos and Simon (1974) reported 44 species of polychaetes from Tampa Bay. Nine of those were also found in St. Louis Bay, and 3 (*Capitella capitata*, *Laeonereis culveri*, and *Streblospio benedicti*) were among the more abundant organisms in both studies. Johnson (1980) listed 25 species from Mobile Bay, Alabama, which were also collected in St. Louis Bay. However, of the 21 most abundant species listed by Johnson, only 5 were found in St. Louis Bay. *Mediomastus*

californiensis was the most abundant benthic macroinvertebrate in both studies but the remaining 4 species (*Diopatra cuprea*, *Glycinde solitaria*, *Neanthes succinea*, and *Paraprionospio pinnata*) were taken relatively infrequently in St. Louis Bay. Species groups reported by Johnson were unlike the groups seen in this study. Sikora et al. (1981) reported 30 taxa from Lake Pontchartrain, Louisiana; however, 2 species of hydrobid gastropods (*Probythinella louisianae* and *Texadina sphinctostoma*) made up 86% of all individuals. Most of those taxa were found in St. Louis Bay but the hydrobids were seen only occasionally. The infauna of Trinity Bay, Texas, (McBee 1975) showed the highest degree of similarity to the benthic community of St. Louis Bay. Thirty species were reported from grab samples in Trinity

Bay and 19 of these were also collected in St. Louis Bay. *Mediomastus californiensis* was most abundant in Trinity Bay as it was in St. Louis and Mobile Bays. Cluster analysis in the Trinity Bay study produced a ubiquitous and abundant species group which was nearly identical to group A of this study. No other group similarities were noted.

ACKNOWLEDGMENTS

The authors wish to thank Dr. John Steen for sharing his insights into dynamics of the estuarine habitat and to Drs. Robert Woodmansee, Edwin Cake, and Richard Heard for their advice and counsel in reviewing the manuscript. Chris Snyder and Martha Chambers assisted with collection and processing of the samples.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.04

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Recommended Citation

Heard, R. W. 1982. Observations on the Food and Food Habits of Clapper Rails (*Rallus longirostris* Boddaert) from Tidal Marshes Along the East and Gulf Coasts of the United States. *Gulf Research Reports* 7 (2): 125-135.

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OBSERVATIONS ON THE FOOD AND FOOD HABITS OF CLAPPER RAILS (*RALLUS LONGIROSTRIS* BODDAERT) FROM TIDAL MARSHES ALONG THE EAST AND GULF COASTS OF THE UNITED STATES

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ABSTRACT The feeding habits of five nominal subspecies of clapper rails (*Rallus longirostris* Boddaert) collected in tidal marshes along the Gulf and Atlantic coasts of the United States are compared. Data on the food from the stomachs of 183 rails were analyzed and the earlier literature critically reviewed. During the warmer months (May through early fall), crabs, predominantly *Uca* spp., comprised the major part of the food items found. Limited data on a few rails collected during late fall and winter, when *Uca* spp. are not usually available, indicate that snails then become a major part of the clapper rail's diet during that part of the year. Earlier studies, which describe the food or feeding habits of clapper rails, are reviewed and the food habits and trophic relationships of some other tidal marsh consumers are discussed. Data from this and previous studies indicate that clapper rails are opportunistic omnivores, and occupy a relatively broad niche within tidal marsh ecosystems. A comparison of available data of the food of five clapper rail subspecies of the eastern United States indicates no distinct differences in their feeding behavior. Differences in the kinds of food eaten appear to simply reflect the types of marsh habitat (fresh, brackish, polyhaline) or geographical location (temperate, subtropical, tropical) in which a particular clapper rail population occurs. The food habits of the king rail are compared with those of the clapper rail and problems concerning the taxonomic status of the "subspecies" of *Rallus longirostris* are briefly discussed.

INTRODUCTION

The purpose of this report is to review and compare the feeding habits of the five nominal subspecies of clapper rails (*Rallus longirostris* Boddaert) endemic to the salt marshes and mangrove swamps of the Atlantic and Gulf coasts of the United States. The information presented here is based on food data obtained in conjunction with a study of clapper rail parasites (Heard 1968a, b, 1970, Deblock and Heard 1969, Byrd and Heard 1970, Nickol and Heard 1970, Brooks and Heard 1977) and a critical review of the published literature. An overview of the trophic relationships of clapper rail subspecies occurring in tidal salt marshes of the eastern United States will be presented. The diets of the king rail and the clapper rail will be compared and discussed. Taxonomic uncertainties concerning the subspecies of the clapper rail also will be briefly discussed.

Historical

The clapper rail, often called the mud or marsh hen, is abundant in the salt marsh and mangrove swamps of the Atlantic and Gulf coasts of the United States. This species and its eggs were a source of food and "sport" to residents along the eastern coast of the United States during the 18th and 19th centuries (Audubon 1840, Bent 1926). Clapper rails are still hunted along much of the Atlantic and Gulf coasts (Oney 1954, Adams and Quay 1958, Bateman 1966, Smith 1967). References to the earlier literature on the food, systematics, natural history, behavior, ecology, and parasites of *Rallus longirostris* subspecies are given by Bent (1926), Oberholser (1937), Adams and Quay (1958), Bate-

man (1965), Heard (1970), and Holliman (1978). Bent (1926) summarized observations by Audubon (1840) and Simmons (1914) on the food and feeding habits of clapper rails. Howell (1928, 1932), Oney (1954), and Bateman (1965) gave additional, more detailed data on the diet of this marsh bird.

There are currently five recognized subspecies of *R. longirostris* known to occur on the Atlantic and Gulf coasts (Ripley 1977). These are the northern clapper rail *R. longirostris crepitans* Gmelin, Wayne's clapper rail *R. longirostris waynei* Brewster, the Florida clapper rail *R. longirostris scotti* Sennett, the mangrove clapper rail *R. longirostris insularum* Brooks, and the Louisiana clapper rail *R. longirostris saturatus* Ridgway (Oberholser 1937, Ridgway and Friedman 1941, Ripley 1977).

Figure 1 presents a map giving the general ranges for these five subspecies. The northern clapper rail *R. longirostris crepitans* is a resident of the more temperate *Spartina-Juncus* marshes. This form is the only one of the five east coast subspecies known to migrate substantial distances. From April to August it nests in marshes from New England southward into Virginia. During the colder months (from late fall to mid-spring) a large part of the population migrates along the Atlantic coast as far south as central Florida (Howell 1932, Stewart 1954). Wayne's clapper rail *R. l. waynei* occurs in *Spartina-Juncus* marshes along the Atlantic coast from North Carolina to east central Florida. Although part of the population shifts southward a few miles during the winter, this "subspecies" is not considered migratory (Oney 1954). The Florida clapper rail *R. l. scotti* occurs along the southern Atlantic coast and the Gulf coast of Florida (Howell 1932) in both *Spartina-Juncus* marshes and mangrove habitats. The mangrove clapper rail *R. l. insularum*

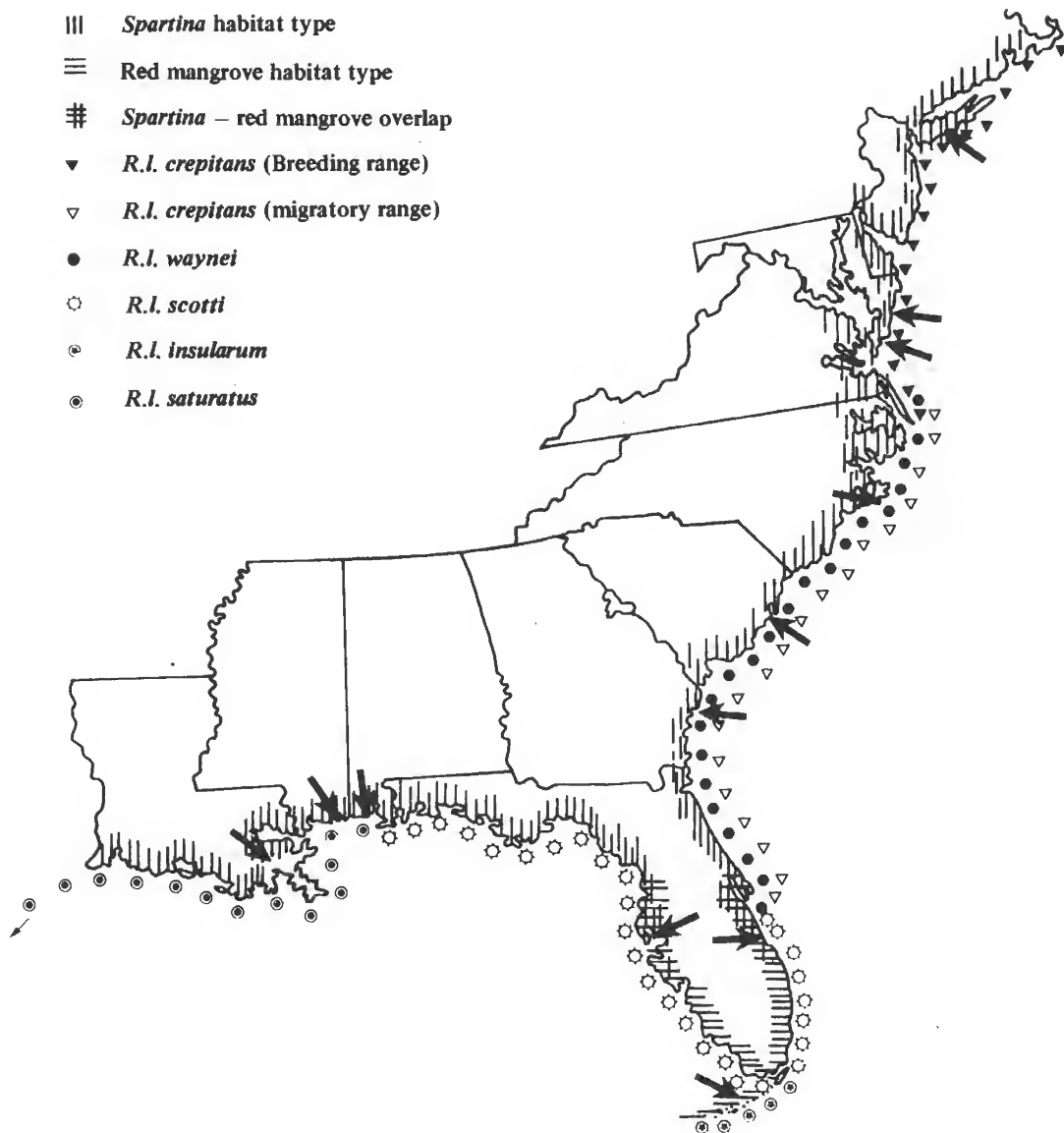


Figure 1. Map showing distribution of the five nominal subspecies of *Rallus longirostris* occurring in salt marshes along the eastern United States. Arrows indicate collecting areas sampled during the present study.

is apparently confined to the polyhaline mangrove swamps of the Florida Keys (Howell 1932, Oberholser 1937). The Louisiana clapper rail *R. l. saturatus*, occurs along the Gulf coast from Alabama to Texas (Howell 1928). Like the Florida clapper rails, this subspecies occurs in *Spartina-Juncus* marshes in the northern Gulf and in mangrove areas in the southern part of its range.

There is relatively little information available on the food and feeding habits of these five "subspecies." Audubon (1840) observed *R. l. crepitans* eating crabs, snails, aquatic insects, small fishes and plants, but he did not specifically identify the food organisms. Stone (1937) mentions that a meadow vole was found in the stomach of a specimen collected at Cape May, New Jersey. In a study of mixed

populations of King and northern clapper rails in Delaware, Meanley and Wetherbee (1962) reported the red-jointed fiddler crab *Uca minax*, and a clam, *Macoma baltica*, as important foods. Information on the food of "*Rallus longirostris*," the northern clapper rail, presented by Martin, Zim, and Nelson (1951) probably refers to *R. l. crepitans*. Howell (1932) lists eight species of crabs and snails from the stomachs of 22 *R. l. waynei* collected in northeast Florida. Oney (1954) examined the contents of 284 stomachs from *R. l. waynei* killed by hunters on the Georgia coast. He found over 30 genera of food organisms and, of the total volume, crabs comprised 74%, snails 14%, and insects 9%. The semi-terrestrial grapsid crab, *Sesarma cinereum*, accounted for 33% of the total volume of food recovered. Adams and Quay (1958) and Shanholtzer (1973) mentioned fiddler crabs (*Uca* spp.) as food for *R. l. waynei*. Howell (1932) listed four species of decapod crustaceans and one species of insect from eight stomachs of *R. l. scotti* collected in western Florida. No studies have been published on the food of the mangrove clapper rail, although Forbush and May (1955) stated that "it probably differs somewhat from other races of clapper rail in feeding habits on account of its quite different environment, the ecological factors in the mangrove swamp being unlike those of the salt marshes of the Atlantic coast." Simmons (1914) made general observations on the diet of *R. l. saturatus* from the Texas coast. Howell (1928) gave information on the food of Louisiana clapper rails from Alabama. In a comprehensive study, Bateman (1965) examined the stomachs of 103 *R. l. saturatus* collected at Grand Terre Island, Louisiana, and identi-

fied nine genera of food organisms. *Uca* sp., *Littorina* sp. and *Sesarma* sp. occurred most frequently (74%, 49%, and 38%, respectively). Holliman (1978) found *Uca* remains and seeds in the stomachs of seven birds collected on the coast of Alabama, and in the same study he also observed a single bird feeding on an unidentified fish.

MATERIALS AND METHODS

Clapper rails from 11 localities (Table 1 and Figure 1) were collected by hand (immature birds and molting adults at high tide only) or with a shotgun. Birds were collected during both high and low tides; however, most of the specimens of *R. l. crepitans* were collected during high tide. Stomachs were removed and examined for food organisms as soon as possible (within 6 hours of collection). Identifications to lowest possible taxon were made with the aid of a dissecting microscope having a magnification range of 6X–50X. Only stomach contents that were reasonably intact or that had diagnostic parts were identified.

RESULTS

Table 1 gives the localities, season, and number of birds of each subspecies examined. Sixty-three (33%) of the 187 stomachs examined were empty. The stomachs of 30 (75%) of the 40 *R. l. crepitans* examined were empty. Nearly all the specimens of this subspecies were collected during high tide, and many were alive for several hours after being collected. These factors probably account for the high percentage of empty stomachs. From 0% to 32% of the stomachs of the other subspecies were empty. Table 2 presents a

TABLE 1.

Number of clapper rails of each subspecies examined during this study with relation to locality and season collected.

Subspecies	State	County	Season	Number of birds examined
<i>R. l. crepitans</i>	New Jersey	Cape May	summer	20
	Maryland	Worcester	summer	10
	Virginia	Accomac	summer	10
<i>R. l. waynei</i>	North Carolina	Carteret	summer	20
			fall	5
			winter	5
	South Carolina	Charleston	summer	5
			summer	15
			fall	15
<i>R. l. scotti</i>	Florida	Pinellas	summer	12
			summer	10
<i>R. l. insularum</i>	Florida	Monroe	summer	10
<i>R. l. saturatus</i>	Alabama	Mobile	summer	10
			summer	10
	Mississippi	Jackson	fall	5
			winter	5
			summer	10
	Louisiana	Jefferson	summer	10
			Total	187

listing of the food organisms found, the percent of stomachs containing each food item, and the total number of birds with empty stomachs.

The food of all five subspecies was essentially the same. Crabs were found in approximately 90% of all the stomachs containing food. The predominant crab genus was *Uca*, occurring in approximately 80% of the stomachs of *R. l. crepitans* and *R. l. insularum* and in approximately 70% of the stomachs of *R. l. waynei*, *R. l. scotti* and *R. l. saturatus*. *Sesarma* species were in approximately 20% of the stomachs of all "subspecies" except *R. l. insularum*.

Mollusks were the next most common food group, occurring in over 25% of the stomachs of *R. l. insularum* and *R. l. saturatus* and in over 15% of the stomachs of the other subspecies. *Littorina irrorata* was the most frequently occurring mollusk species followed by *Melampus bidentatus*.

Other food items occurred less frequently. Insects made up a small part of the diet in all five subspecies but were most frequent in *R. l. insularum* and *R. l. waynei*. Amphipods were found in a few stomachs of all subspecies except *R. l. saturatus*. Plant material was present in some stomachs of *R. l. waynei*, *R. l. insularum*, and *R. l. saturatus*. Polychaetes were identified occasionally among the food items of *R. l. waynei* and *R. l. saturatus*. Shrimp and fish remains were found only in the stomach contents of *R. l. saturatus*.

DISCUSSION

Table 3 lists the food organisms or types which have been reported in previous studies for the five eastern subspecies of *R. longirostris*. Some of the specific names for the food organisms listed by Howell (1932) are now out of date or appear to have been confused with other closely related forms. In Table 3, suggested corrections and additions to the scientific names appear in brackets following the original designation. In cases when only the genus name was given and only one species of the genus is present in the salt marsh habitat, the full scientific name is added. Questionable records are followed by a question mark in brackets. Howell's report of "*Palaemonetes exilipes*" in the diet of *R. l. scotti* from the northwestern coast of Florida probably refers to *P. pugio*, a brackish-water species common in the salt marshes of that area. The name *P. exilipes* has been confused with those of two freshwater prawns, *P. kadiakensis* and *P. paludosus*; it is now considered a synonym of the latter (Holthuis 1952). "*Uca pugnax rapax*" is now considered *Uca rapax* (Tashian and Vernberg 1958). Howell's (1932) records of *Uca* ("*pugnax*") *rapax*, *Sesarma recordii*, and *Neopanope packardii* as food of *R. l. waynei* in northeastern Florida are questionable. These three species of crabs are more characteristic of southern Florida and are not known to occur in northeastern Florida (Tashian and

TABLE 2.
Food from stomachs of *Rallus longirostris* collected during the present study giving the % occurrence of each food item for the five subspecies examined.

"Subspecies"	<i>crepitans</i>	<i>waynei</i>	<i>scotti</i>	<i>insularum</i>	<i>saturatus</i>	All
No. stomachs with food	10	51	18	10	35	124
ARTHROPODA	100.0	100.0	94.4	90.0	74.0	91.1
CRUSTACEA	90.0	96.1	94.4	90.0	74.0	89.5
DECAPODA	90.0	94.1	88.9	90.0	74.0	87.9
<i>Uca</i>	80.0	68.6	66.7	80.0	71.4	71.0
<i>U. pugnax</i>	80.0	52.9	11.1	—	—	29.8
<i>U. longisignalis</i>	—	—	38.9	—	40.0	16.9
<i>U. pugilator</i>	—	11.8	—	—	—	4.8
<i>U. rapax</i>	—	—	16.7	60.0	—	7.2
<i>U. panacea</i>	—	—	—	—	28.6	8.1
<i>U. spectiosa</i>	—	—	—	20.0	—	1.6
<i>Sesarma</i>	20.0	21.6	27.8	—	14.3	18.5
<i>S. reticulatum</i>	20.0	21.6	27.8	—	11.4	17.7
<i>S. cinereum</i>	—	5.9	—	—	2.9	3.2
<i>Aratus pisonii</i>	—	—	11.1	20.0	—	3.2
<i>Eurytium limosum</i>	—	2.0	16.7	—	5.7	4.8
<i>Panopeus herbstii</i>	—	2.0	—	—	—	0.7
<i>Rhithropanopeus harrisi</i>	—	—	—	—	2.9	0.7

TABLE 2. (Continued)

Food from stomachs of *Rallus longirostris* collected during the present study giving the % occurrence of each food item for the five subspecies examined.

Food Items	"Subspecies"	<i>crepitans</i>	<i>waynei</i>	<i>scotti</i>	<i>insularum</i>	<i>saturatus</i>	All
	No. stomachs with food	10	51	18	10	35	124
SHRIMPS		—	—	—	—	2.9	0.7
<i>Palaemonetes pugio</i>		—	—	—	—	2.9	0.7
AMPHIPODS	10.0	15.7	16.7	10.0	—	—	10.5
<i>Orchestia grillus</i>	10.0	15.7	16.7	—	—	—	9.7
<i>Orchestia</i> sp. (undescribed)	—	—	—	10.0	—	—	0.7
INSECTS	10.0	15.7	5.6	20.0	2.9	10.5	5.6
<i>Orchelimum fidicinum</i>	—	11.8	—	—	2.9	—	5.6
unidentified insects	10.0	7.8	5.6	10.0	—	—	0.6
ants	—	—	—	10.0	—	—	0.6
MOLLUSKS	20.0	17.6	16.7	30.0	28.6	21.8	12.1
<i>Littorina</i>	10.0	5.9	5.6	10.0	25.7	10.5	0.6
<i>L. irrorata</i>	10.0	5.9	5.6	—	25.7	—	0.6
<i>L. angulifera</i>	—	—	—	10.0	—	—	0.6
<i>Melampus</i>	20.0	13.7	11.1	20.0	5.7	12.1	6.5
<i>M. bidentatus</i>	10.0	13.7	—	—	5.7	—	3.2
<i>M. coffeus</i>	—	—	11.1	20.0	—	—	0.7
<i>Guekensia demissa</i> (juv)	—	—	5.6	—	—	—	0.7
<i>Tagelus plebeius</i> (juv)	—	—	5.6	—	—	—	0.7
POLYCHAETES	—	15.7	—	—	2.9	7.3	7.3
<i>Nereis succinea</i>	—	15.7	—	—	2.9	—	1.6
FISH	—	—	—	—	5.7	0.7	0.7
<i>Lagodon rhomboides</i>	—	—	—	—	2.9	—	0.7
unidentified remains	—	—	—	—	2.9	—	0.7
PLANT MATERIAL	—	5.9	—	20.0	17.1	8.7	6.5
Unidentified	—	3.9	—	20.0	17.1	—	0.7
Acorns (live oak)	—	2.0	—	—	—	—	0.7
	No. empty stomachs	30	24	4	—	5	63

Vernberg 1958, Abele 1972, 1973). The record of *U. rapax* probably refers to the closely related *U. pugnax* and that of *S. recordii* to the closely related *S. cinereum*. *Neopanope packardii* was probably a misidentification of *Eurypanopeus depressus* or *Panopeus herbstii* which are superficially similar. *Uca pugnax*, *S. cinereum*, *E. depressus* and *Panopeus herbstii* are common in the salt marsh habitats of northeastern Florida.

Data from this study and from those of Oney (1954) and Bateman (1965) indicate that crabs of the genera *Uca* and *Sesarma* are the most commonly occurring food organisms in the diet of clapper rails from the Atlantic and Gulf coasts. *Uca* spp. were the most frequently encountered crabs in this study and in Bateman's (1965) study of *R. l. saturatus*. In Oney's (1954) study of *R. l. waynei*, however, *S. cinereum* was the most common crab found. Both seasonal and tidal factors may explain this difference. During the

colder months *Uca* spp. are inactive and remain in their burrows (Teal 1958), where they are not readily accessible to clapper rails. Oney's observations were made on birds killed by hunters during the fall, and some of these specimens may have been collected during cold periods, when *S. cinereum* would be more easily obtained than *Uca*. Tides may also affect the relative availability of *S. cinereum* and *Uca* spp. Almost all marsh hen hunting in Georgia is done during very high tides when rails have less cover and when hunters can take their boats into the marshes (Oney 1954). *Sesarma cinereum* is more terrestrial than *Uca* spp. and *S. reticulatum*, living primarily in upper intertidal and supratidal areas or in association with large rafts of dead *Spartina*. During high tides it generally stays out of the water on top of *Spartina* rafts or along shore, where it is the most abundant crab present and is more vulnerable to predation. Observations made during this study indicate that clapper

TABLE 3.

A synoptic listing of food items previously reported from the five subspecies of *Rallus longirostris* from salt marshes along the Atlantic and Gulf coasts of the United States. Suggested corrections and additions to scientific names are in brackets. The reference or references for each food item follow it (separated by a hyphen).

Rallus longirostris crepitans

Crabs: "crabs"—Audubon (1840); *Uca minax*—Meanley and Wetherbee (1962).

Mollusks: "snails"—Audubon (1840); *Macoma baltica*—Meanley and Wetherbee (1962).

Insects: "aquatic insects"—Audubon (1840).

Vertebrates: fishes (minnows, fry)—Audubon (1840); *Microtus* [= *M. pennsylvanicus*]—Stone (1937).

Vegetation: unidentified plant material—Audubon (1840).

Rallus longirostris waynei

Crabs: "crabs"—Oney (1954); *Callinectes* sp. [= *Callinectes sapidus*]—Oney (1954); *Eurytium limosum*—Oney (1954); *Panopeus herbstii*—Howell (1932), Oney (1954); Pinnotheridae (unidentified)—Oney (1954); *Sesarma cinereum*—Oney (1954); *Sesarma reticulatum*—Howell (1932), Oney (1954); *Uca* (sp. or spp.)—Adams and Quay (1958); Oney (1954); *Uca pugilator*—Oney (1954); *Uca pugnax*—Shanholtzer (1973); *Uca pugnax rapax* [= *Uca pugnax*?]—Howell (1932).

Shrimp: *Penaeus setiferus*—Oney (1954); *Palaemonetes* sp. [= *Palaemonetes pugio*]—Oney (1954).

Mollusks: *Ilyanassa* (= *Nassarius*) *obsoleta*—Howell (1932), Oney (1954); *Littorina irrorata*—Howell (1932), Oney (1954); *Melampus* sp. [= *M. bidentatus*]—Oney (1954); Molulidae [sic?] (clams)—Oney (1954); *Polygyra* sp.—Oney (1954).

Marine worms: *Nereis* sp. [= *Nereis succinea*?]—Oney (1954).

Insects: *Acanthopallus* sp.—Oney (1954); Acrididae (unidentified)—Oney (1954); *Anisotabis* sp.—Oney (1954); *Apis mellifera*—Oney (1954); Balattidae (unidentified)—Oney (1954); *Crematogaster* sp.—Oney (1954); *Gambusia bituminosus*—Oney (1954); Gryllidae (unidentified)—Oney (1954); *Gryllus assimilis*—Oney (1954); *Hylobius pales*—Oney (1954); Hymenoptera (unidentified)—Oney (1954); Ichneumonidae (unidentified)—Oney (1954); *Leptoglossus phyllopus*—Oney (1954); *Metanoplus* sp.—Oney (1954); *Neoconocephalus triops*—Oney (1954); *Scapteriscus* sp.—Oney (1954); *Schistocerca americana*—Oney (1954).

Spiders: *Clubiona* sp.—Oney (1954); *Lyeosa* sp.—Oney (1954).

Vertebrates: *Fundulus* sp.—Oney (1954); Poeciliidae (unidentified)—Oney (1954).

Plant material: *Spartina alterniflora*—Oney (1954).

Rallus longirostris scotti

Crabs: *Callinectes sapidus*—Howell (1932); *Neopanopeus packardii* [?]—Howell (1932); *Rhithropanopeus harristii*—Howell (1932); *Sesarma ricordi* [= *Sesarma cinereum*?]—Howell (1932); *Uca pugnax* [= *Uca longisignalis*]—Howell (1932).

Shrimp: *Palaemonetes exillipes* [= *Palaemonetes pugio*]—Howell (1932).

Insects: "grasshoppers"—Howell (1932); *Anisotabis maritima*—Howell (1932); "beetles" [Coleoptera]—Howell (1932); "butterfly cocoons"—Howell (1932).

Rallus longirostris insularum

(No previous food records)

Rallus longirostris saturatus

Crabs: "crabs"—Simmons (1914), Howell (1928); *Panopeus* sp. [= *Panopeus herbstii*]—Bateman (1965); *Sesarma* sp.—Bateman (1965); "Fiddler or fighting crabs" [= *Uca* (sp. or spp.)]—Simmons (1914).

Hermit crabs: *Clibanarius* sp. [= *Clibanarius vittatus*]—Bateman (1965).

Shrimp: "shrimp"—Howell (1928).

Mollusks: "clams"—Bateman (1965); "slugs"—Simmons (1914); "snails"—Simmons (1914); *Littorina* sp. [= *Littorina irrorata*]—Bateman (1965); *Melampus* sp. [= *M. bidentatus*]—Bateman (1965); *Odostoma* sp. [= *Hydrobiidae*?]—Bateman (1965).

Marine worms: "marine worms"—Howell (1928, 1932).

Insects: "aquatic insects"—Simmons (1914); "grasshoppers"—Simmons (1914); *Sphenophorus* sp.—Bateman (1965); Tettigoniidae (unidentified)—Bateman (1965); *Belostoma* sp.—Bateman (1965).

Vertebrates: fishes (minnows, fry)—Howell (1928), Bateman (1965); diamondback terrapin [= *Malaclemys terrapin*]—Simmons (1914).

Plant material: unidentified plant material—Bateman (1965); seeds—Simmons (1914).

rails feed throughout the tidal cycle, although apparently most feeding occurs during low tide. Birds collected at low tide during the warmer months had been feeding largely on *Uca* spp. and to a lesser extent on *S. reticulatum*. In Georgia, during this study, the three birds that had been feeding on *S. cinereum* were collected at high tide.

My findings agree with those of Oney (1954) and Bateman (1965) in that marsh snails of the genera *Littorina* and *Melampus* appear to be the second most abundant component of the marsh hen's diet. Seasonal observations on *R. l. waynei* and *R. l. saturatus* indicate that these mollusks may be major food items during cold periods when *Uca* and other marsh crabs are less accessible.

Salt marshes support relatively large numbers of insects (Davis and Gray 1966). Oney (1954) reported a much

greater number of insects from the stomachs he examined than did Bateman (1965), earlier workers, and this study. Again, tide conditions may have influenced Oney's data, since high tides reduce the cover, thereby concentrating many of the insect species and making them more vulnerable to predation.

Polychaete worms were not often found in the gut and stomach contents of clapper rails examined during this study or those from earlier studies; however, they may be more important in the diet of clapper rails than this or previous studies indicate, especially during the cold months. *Nereis* (*Neanthes*) *succinea*, a relatively large worm with distinctive mouth parts, is the only form that has been identified from the rail stomachs examined. It is possible, however, that the macerated remains of smaller polychaetes, lacking hard

mouth parts, could have been overlooked. On numerous occasions during low tides, I have observed Wayne's clapper rails feeding along mud banks and in creek beds in *Spartina-Juncus* marshes. The rails were often actively probing in the substrata with their bills. On several occasions I sieved the mud-sand sediment from areas where the birds had been probing and found small, fragile polychaetes, principally *Scolopis fragilis* and *Heteromastix filiformis*.

Vertebrates have rarely been reported in the stomach contents of clapper rails; however, indirect data from a study of helminth parasites of the clapper rail indicate that fish are of some importance in their diets (Heard 1970, unpublished data). I removed a 5-cm-long pinfish, *Lagodon rhomboides*, from the bill of an adult *R. l. saturatus* collected at Dauphin Island, Alabama. Pinfish are wide, heavy-bodied fish, and it seems doubtful that a clapper rail could swallow a 5-cm specimen without first tearing it apart. Holliman (1978) also observed a clapper rail in the same general area of Dauphin Island feeding on an unidentified fish. The only published record of a mammal in the diet of clapper rails is that of Stone (1937) who reported that a meadow vole (*Microtus* sp.) was recovered from the stomach of *R. l. crepitans* collected in New Jersey. Sibley (personal communication, 1962) has observed California clapper rails (*R. l. obsoletum*) feeding on "small mice" in the marshes of San Francisco Bay.

Plant matter, principally seeds, is eaten by clapper rails, but it apparently is not an important part of their overall diets. Martin, Zim, and Nelson (1951) presented seasonal data based on the examination of 278 clapper rails, which indicated a larger consumption of plant food during the winter. In seasonal food studies of king rails, Martin, Zim, and Nelson (1951) and Meanley (1956, 1969) also reported a higher percentage of plant food from the stomachs of birds collected during the winter months, a situation which Meanley (1969) attributed largely to the scarcity of animal food during the winter.

All five subspecies of clapper rails studied ate basically the same kinds of food organisms—crabs, snails, and to a lesser extent, insects, polychaetes, bivalves, fishes, and plant material. There are some differences in dietary composition due to zoogeography and habitat type (*Spartina-Juncus* or mangrove).

The more temperate *Spartina* marshes of the east coast and of the northern Gulf coast are interrupted by the more tropical mangrove regions of southern Florida. Accordingly, some endemic salt marsh animals such as *Uca minax*, *Sesarma cinereum*, *S. reticulatum*, *Littorina irrorata*, *Geukensia* (= *Modiolus*) *demissa*, and *Orchestia grillus* apparently have disjunct ranges on the Gulf and Atlantic coasts

(Williams 1965, Abele 1973, Abbott 1974, Bousfield 1973). The mud fiddler crab *Uca pugnax* is confined to the salt marshes of the Atlantic seaboard, whereas its ecological cognate, *U. longisignalis*, is endemic to the salt marshes of the Gulf of Mexico (Salmon and Atsides 1968). These two species appear to occupy similar niches within their respective ranges.

Other food organisms of clapper rails, including *Uca pugilator*, *U. speciosa*, *U. rapax*, *Eurytium limosum*, *Rhithropanopeus harrisi*, *Panopeus herbstii*, *Melampus bidentatus*, and *Nereis* (N.) *succinea*, occur in both salt marsh and mangrove habitats (Crane 1975, Morrison 1958, 1964, Pettibone 1963, W. E. Odum 1971, Heard, unpublished observations). The range of the xanthid marsh crab *E. limosum* apparently extends no further northward than South Carolina (Williams 1965). *Uca rapax* is now known to occur on the Atlantic coast north of central Florida (Tashian and Vemberg 1958). Thurman (1973) reported that in the Gulf *Uca rapax* was apparently absent from the coasts of eastern Alabama and northwestern Florida. He also reported that *U. speciosa* occurred along the Gulf coast from Mississippi to the southern tip of Florida. *Uca pugilator* has a continuous range from New England into west Florida. A recently described cognate species, *U. panacea*, previously thought to be *U. pugilator*, replaces it west of Pensacola (Thurman 1973, Novak and Salmon 1974). *Nereis* (N.) *succinea*, *Melampus bidentatus*, *Panopeus herbstii*, and *Rhithropanopeus harrisi* occur throughout the coastal region of the southeastern United States; however, *R. harrisi*, a low-salinity species, apparently does not occur in the polyhaline waters of the Florida Keys.

Aratus pisonii, *Littorina angulifera*, and *Melampus coffeae* are tropical forms closely associated with mangrove habitats (Rathburn 1918, Morrison 1964, Hartnoll 1965, Abbott 1974, Thomas 1974). Accordingly, they only occurred in the stomachs of clapper rails collected from areas in or adjacent to mangrove swamps along the southern half of peninsular Florida.

Habitat variation also occurs within the tidal marshes or mangrove swamps in the same geographical area (e.g., an estuarine system). For example, along the southeastern Atlantic seaboard the lower reaches of estuaries are generally characterized by extensive *Spartina* marshes with an associated mesohaline fauna made up of species such as *Uca pugnax*, *U. pugilator*, *Eurytium limosum*, *Orchestia grillus*, *Melampus bidentatus*, *Modiolus demissus*, and *Littorina irrorata*. In contrast, in the oligohaline upper reaches of these estuaries, *Spartina* marshes are largely replaced by *Juncus* marshes. Some of the characteristic organisms occurring in this type of habitat are *Uca minax*, *R. harrisi*, *Polymesoda caroliniae*, *Cyrenoidea floridana*, *Orchestia uhleri*, and *Detracia floridana*. Similar conditions occur in other tidal

marshes and mangrove swamps along the Atlantic and Gulf coasts. Since clapper rails occur in the tidal marshes and mangrove swamps throughout the eastern United States it can be assumed that their food varies accordingly.

Trophic level

It is virtually impossible with the data now available to assign salt marsh consumers such as the clapper rail to specific or well-defined trophic levels. This is due to several factors: (1) feeding habits which are incompletely documented; (2) omnivorous feeding habits; (3) the still uncertain trophic position of "organic detritus" and (4) the seasonal availability of various food organisms.

Both *Spartina-Juncus* and mangrove systems have been described as having food webs largely based on detritus (E. P. Odum 1961, 1971, Teal 1958, 1962, Odum and de la Cruz 1967, W. E. Odum, 1971, Wass and Wright 1969, Day et al. 1973, Thomas 1974). The definitions, significance, origins, and overall conceptual problems concerning "organic detritus" in marine and estuarine systems have been discussed by Darnell (1964, 1967a, 1967b), Newell (1965), E. P. Odum (1971), Mann (1972), and Saunders (1972). Darnell (1967b) defined organic detritus as "all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species." As understood by W. E. Odum (1971), the definition "includes materials which are sorbed upon the basic particle, bacteria, fungi, and protozoa, along with adsorbed dissolved organic and inorganic compounds. The entire particle and its sorbed load should be considered as a single unit. . . a small ecosystem within a larger system."

Although incompletely known, the food webs and energy flow models proposed for *Spartina-Juncus* systems (Teal 1962) and for mangrove systems (W. E. Odum 1971, W. E. Odum and Heald 1972) appear to be relatively similar. On this basis, and on the similarity of the types of food eaten, it can be assumed that clapper rails associated with both these habitats generally have similar trophic relationships. In his energy flow model for a Georgia salt marsh ecosystem, Teal (1962) categorized clapper rails as "secondary consumers" (primary carnivore).

In view of the data now available on estuarine food webs and in terms of the second law of thermodynamics as applied to biological systems by Linderman (1942), clapper rails would necessarily occupy a trophic level higher than that of a secondary consumer. Darnell (1964, 1967a, 1967b) and E. P. Odum (1971, p. 74) have pointed out that the "detritus consumer" (detritivore) is quite different trophically from the "primary consumer" or "herbivore" of the grazing food chain. The primary consumer derives its energy directly from plant matter (i.e., first trophic level) while the detritus consumer may obtain its energy from food material derived from as many as three or more trophic levels. The foods eaten by clapper rails cover a wide trophic spectrum and it

would seem from the trophic data now available that the clapper rail's overall trophic position would be that of a secondary carnivore.

Based on unpublished studies and observations on the foods of salt marsh consumers, I have found that vertebrates such as the seaside sparrow *Ammodramus maritima*, sora rail *Prozana carolina*, rice rat *Oryzomys palustris*, and raccoon *Procyon lotor* have diets that are generally similar or overlap considerably that of the clapper rail during all or part of the year. Though niche-partitioning occurs among these and other salt marsh omnivores, it has not been well documented and remains a fertile area for further ecological research. A complex of subtle temporal and spatial factors, in conjunction with predator-prey size and size classes, must be understood before any meaningful description of food-resource partitioning among salt marsh omnivores and carnivores can be presented.

It should be noted that clapper rails serve as a food source for other vertebrate predators. These include the alligator, marsh hawk, mink, otter, and man (Smith 1967, Bateman 1965, Heard, unpublished observ.).

Comparison with food habits of the king rail

Whether or not the king rail *Rallus elegans* Audubon, a predominantly freshwater form, is conspecific with the similar and closely related *R. longirostris* Boddaert, has been debated since the writings of Wilson and Audubon (Audubon 1840, Bull 1964, Mayr and Short 1970). Because the king rail's range overlaps that of the clapper rail, a comparison of these two birds' food habits was made. Since Bent's (1926) review, a number of authors have reported these two forms occurring together in brackish tidal marshes (Oberholser 1937, 1938, Lowery 1955, Tomkins 1958, Meanley and Wetherbee 1962, Meanley 1965, 1969), and in Delaware Bay they have been observed interbreeding (Meanley and Wetherbee 1962). Oberholser (1937) discussed the systematic position of these two rails and concluded, "... it seems best, at least for the present, to consider these birds as representing two species, *Rallus elegans* consisting of two subspecies, and *Rallus longirostris*, made up altogether of 25 races (=subspecies)."

Because the king rail's range overlaps that of the clapper rail, a comparison of their food habits was made to determine if any important differences could be detected with the limited amount of published data available. King rails are primarily associated with freshwater habitats; however, they appear to have the same kind of omnivorous feeding habits as do clapper rails from tidal marshes. Meanley (1956, 1965, 1969) gave information on the food of king rails collected from a number of different habitats in the eastern half of the United States. As in the case of the clapper rail, his data indicate that the composition of the king rail's diet simply reflects the presence of the most common organisms of food size characteristic of the particular habitat from

which the birds were collected. Typical foods of king rails from freshwater areas were crayfish, frogs, insects, fishes, and plant seeds. Part of Meanley's observations, however, were made in a brackish marsh area on Delaware Bay where mixed populations of king and clapper rails occurred. In this estuarine habitat the diet of both species of rails was essentially the same, consisting largely of a fiddler crab (*Uca minax*) and a clam (*Macoma baltica*). I have also observed king and clapper rails feeding together during the winter months on small fishes and invertebrates in brackish marshes near Ocean Springs, Mississippi.

Taxonomic problems in the clapper rail complex

The taxonomic status of the "subspecies" of *Rallus longirostris* is unclear. The definitions of terms such as "geographic races," "subspecies," and even "species" are complex and accordingly more difficult to properly define and conceptualize (Mayr 1970, Scudder 1974). The taxonomy of the clapper rail and its "subspecies" is an example of this kind of systematic problem.

Although the five nominal subspecies of *R. longirostris* investigated during this study appear to breed in more or less specific geographical areas, interbreeding undoubtedly occurs in the areas of overlap in North Carolina, Florida, and Alabama. Many of 25 "subspecies" reviewed by Oberholser (1937) were described from relatively few specimens. In fact, a number of the "subspecies" descriptions were based on less than ten birds, and in the cases of *R. l. crassirostris* Lawrence, *R. l. belizensis* Oberholser, and *R. l. nayartensis* McLellan, only a single specimen was studied (Oberholser 1937). The "subspecies" of clapper rails were separated by Oberholser (1937) primarily on subtle differences in their color patterns or on minor differences in body measurements. I have observed considerable variation in color patterns and body sizes of adult birds of the same sex collected together. Such variation was particularly evident in the clapper rails I examined from Tampa Bay, a transition-area where both mangrove and *Spartina* marshes occur. In the mesohaline marshes at Cape Romane, South Carolina, young-of-the-year birds (12–16 weeks old) were distinctly larger and heavier than adults taken in the collecting sites from other states. Additionally, the ranges of the five subspecies from the eastern United States, with the possible exception of *R. l. insularum*, do not appear to be clearcut or, as for *R. l. scotti* and *R. l. saturatus*, to relate to the basic *Spartina-Juncus* or mangrove habitat types.

The information available on the food and feeding habits of clapper rails, king rails, and their nominal subspecies occurring along the Atlantic and Gulf coasts of the United States indicates that there are no distinct differences in their feeding behavior. Differences in kinds of food eaten simply appear to reflect the types of marsh habitat (fresh, brackish,

polyhaline) or geographical location (temperate or tropical) where a particular clapper rail population occurs. Accordingly, the clapper rail should be classified trophically as an opportunistic omnivore having a relatively broad niche within the marsh ecosystem in which it resides.

The facts that clapper and king rails interbreed and have the same feeding habits where their populations overlap (Meanley and Wetherbee 1962, Meanley 1965, Meanley 1969, present study) justify considering them as subspecies of *Rallus longirostris*, a designation given them by Mayr and Short (1970) and followed by Wass (1972) and Ripley (1977). If this reasoning is followed, the other forms which have been considered subspecies of the clapper rail (sensu Ripley 1977) might then fall into the category of "geographical races." Recognizing their close similarity, Bull (1964) considered the king and clapper rail to form a "superspecies"; however, such a designation, unless concisely defined, has dubious taxonomic merit. Ripley (1977) considered the king rail a "subspecies" of *R. longirostris*; however, he also recognized all of the other named "subspecies" as valid taxons. Additional research using refined ecological, genetic, and behavioral techniques will be needed before the ecophenotypic, taxonomic and systematic relationships of the clapper rail complex can be fully understood. Notwithstanding qualitative differences in their size, body measurements and color patterns, the recognition of five distinct subspecies of *Rallus longirostris* from the coast of the eastern United States does not appear to be supported by available information on their ecology, reproductive behavior, or food habits.

ACKNOWLEDGMENTS

I wish to express my appreciation to B. Heard for her help and encouragement during the preparation of the manuscript and to D. E. Norris and R. M. Overstreet for their interest and support. Sharon Wilson and Lucia O'Toole expertly typed the drafts and final manuscript and Joan Durfee helped in proofing.

The collection and examination of most clapper rail specimens used in this study were supported in part by an appropriation from the Congress of the United States to the Southeastern Cooperative Wildlife Disease Study, School of Veterinary Medicine, University of Georgia, Athens, Georgia. Funds were administered and research coordinated by the Bureau of Sport Fisheries and Wildlife, Department of the Interior, through Contract No. 14-16-0008-676. Further support for collection of additional data and preparation of the manuscript was provided by the Mississippi-Alabama Sea Grant Consortium under U.S. Department of Commerce's NOAA, Office of Sea Grant Programs Grant No. 04-8-M01-92.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.05

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Recommended Citation

Overstreet, R. M. and R. W. Heard. 1982. Food Contents of Six Commercial Fishes from Mississippi Sound. *Gulf Research Reports* 7 (2): 137-149.

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FOOD CONTENTS OF SIX COMMERCIAL FISHES FROM MISSISSIPPI SOUND¹

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ABSTRACT Specific dietary contents from six fishes collected in Mississippi Sound are recorded. In order of their importance, primary components grouped in major taxonomic categories were fishes, penaeid shrimps, and other crustaceans for *Cynoscion nebulosus*; crustaceans and fishes for *C. arenarius*; fishes and crustaceans for *C. nothus*; crustaceans, pelecypods, and polychaetes for *Pogonias cromis*; crustaceans, molluscs, polychaetes, and fishes for *Archosargus probatocephalus*; and fishes and penaeid shrimps for *Paralichthys lethostigma*. Principal items in the diets of most of the fishes included *Anchoa mitchilli*, *Penaeus aztecus*, *P. setiferus*, and *Callinectes sapidus*. Those crustaceans show that competition exists for commercial shellfishes in Mississippi Sound. Ratios among the different dietary items vary, according at least to species of fish, length of fish, season, specific location, and abundance of available prey. Some of these variations are documented and are additionally related to selected findings by other authors sampling different localities. We suggest that examination of food items in *Archosargus probatocephalus* can serve as a practical means to sample and assess seasonal prevalence and abundance of a wide range of invertebrates throughout different habitats in Mississippi Sound and elsewhere.

INTRODUCTION

Mississippi Sound offers a variety of habitats in which commercial fishes can feed. Examination of food contents of the red drum and Atlantic croaker (Overstreet and Heard 1978a, 1978b) has already indicated that those two fishes feed on organisms from a number of different habitats in and adjacent to the Sound. This paper lists specific food contents of the spotted seatrout, *Cynoscion nebulosus*; sand seatrout, *C. arenarius*; silver seatrout, *C. nothus*; black drum, *Pogonias cromis*; sheepshead, *Archosargus probatocephalus*; and southern flounder, *Paralichthys lethostigma*, for the first time from Mississippi Sound. Knowledge concerning the food of these fishes, based on ontogenetic, temporal, and spatial relationships, allows a better perception of predator biology and, consequently, provides a better means to manage the respective fisheries. Our information demonstrates that commercial finfishes competed for prey. Prey often constituted one of several commercially important fin- or shellfishes. We also present pertinent references that deal with food and feeding habits of the six fishes.

MATERIALS AND METHODS

Most of the fish were collected by trammel nets and examined specifically for food contents. Others were caught by trawl or by hook and line, and the contents were removed from some while examining those fish for other purposes. All fish were maintained on ice until examined. Their stand-

ard lengths (SL) were measured and their food contents either identified when removed or placed in 10% formalin for future identification. Rather than being restricted solely to environmentally derived, microbially degraded, organic matter, the term "detritus" in this paper may include also partially digested animals or plants.

RESULTS

The number of each fish species examined and the number containing food are listed in Table 1 along with the frequency of occurrence of specific dietary items for each fish. The sheepshead, which fed on a minimum of 113 identifiable items, had the most diverse diet. Specific data combined into general taxonomic groups, when sample size of the six predators was sufficient, reveal differences in food contents according to length of fish and season (Tables 2-6).

Fishes and crustaceans occurred frequently in the diets of all three seatrouts, with about twice as many fish as crustaceans in both *C. nebulosus* and *C. nothus* (Table 2). A greater percentage of *C. arenarius* had crustaceans present when compared with percentages for the other two seatrouts, and the percentage increased with fish-length.

Seasonality influenced the diet of *C. nebulosus* as exemplified by the presence of the often abundant bay anchovy, *Anchoa mitchilli*. The bay anchovy occurred infrequently in the seatrout's food contents during spring when other fishes were common prey (Table 3). The spotted seatrout, especially large individuals, contained more polychaetes during winter than during other seasons; "detritus" also occurred commonly in the seatrout's stomach and intestine during that period.

Both *Pogonias cromis* and *Archosargus probatocephalus* fed on a great variety of dietary items, especially benthic ones. The diet of *A. probatocephalus* was influenced by whether the sheepshead was feeding near barrier islands

¹The study was conducted in cooperation with the U.S. Department of Commerce, NOAA, National Marine Fisheries Service under PL 88-309, Project No. 2-325-R and Office of Sea Grant, Mississippi-Alabama Sea Grant Program, grant no. NA81AA-D-0050, MASGP-81-023.

TABLE 1.

Percentage of occurrence of different food items in the digestive tracts of selected fishes from Mississippi Sound.

	Species of fish						
	<i>Cynoscion nebulosus</i>	<i>Cynoscion arenarius</i>	<i>Cynoscion nothus</i>	<i>Pogonias cromis</i>	<i>Archosargus probatocephalus</i> Inshore	<i>Archosargus probatocephalus</i> Near islands	<i>Paralichthys lethostigma</i>
Number fish examined	373	108	25	15	77	65	212
Number fish with food	340	74	12	15	63	62	97
Food item	Percentage of occurrence in fish with food item						
Foraminiferan (unidentified)	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Cnidarians							
<i>Calliactis tricolor</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Clione</i> sp.	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Hydroid remains	0.3	0.0	0.0	0.0	15.9	6.5	0.0
Unidentifiable coelenterate	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Sipunculoidean	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Polychaetes							
<i>Chaetopterus variopedatus</i>	0.0	0.0	0.0	0.0	0.0	6.5	0.0
<i>Chaetopterus</i> tube remains	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Diopatra cuprea</i>	0.6	0.0	0.0	0.0	1.6	11.3	0.0
<i>Glycera americana</i>	0.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nereis (Neanthes) succinea</i>	5.6	0.0	0.0	6.7	15.9	0.0	0.0
<i>Nereis</i> sp. (unidentifiable)	1.5	0.0	0.0	0.0	0.0	3.2	0.0
<i>Pectinaria gouldii</i>	0.0	0.0	0.0	0.0	1.6	3.2	0.0
<i>Polydonte lupina</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Spiochaetopterus oculatus</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Siheneleis boa</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
Unidentifiable maldanid	0.0	0.0	0.0	0.0	1.6	9.7	0.0
Unidentifiable polychaete	0.6	0.0	0.0	13.3	3.2	6.5	2.1
Gastropods							
<i>Anachis</i> cf. <i>obesa</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Anachis</i> sp.	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Cantharus cancellarius</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Crepidula plana</i>	0.0	0.0	0.0	0.0	3.2	1.6	0.0
<i>Crepidula</i> sp.	0.0	0.0	0.0	0.0	3.2	0.0	0.0
<i>Nassarius acutus</i>	0.0	0.0	0.0	0.0	7.9	21.0	0.0
<i>Neritina usnea</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Olivella mutica</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Oliva sayana</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Polinices duplicata</i> egg case	0.0	0.0	0.0	0.0	0.0	4.8	0.0
<i>Seila</i> cf. <i>adamsi</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Turbonilla</i> sp.	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Tectonatica pusilla</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
Unidentifiable nudibranch	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Unidentifiable gastropod	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Gastropod operculum	0.0	0.0	0.0	0.0	1.6	0.0	0.0
Pelecypods							
<i>Abra aequalis</i>	0.0	0.0	0.0	0.0	1.6	8.1	0.0
<i>Amygdalum papyria</i>	0.0	0.0	0.0	6.7	4.8	0.0	0.0
<i>Anadara transversa</i>	0.0	0.0	0.0	6.7	0.0	1.6	0.0
<i>Anadara</i> sp.	0.0	0.0	0.0	0.0	3.2	4.9	0.0
<i>Astarte nana</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Atrina</i> sp.	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Brachidontes exustus</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
<i>Dinocardium robustum</i>	0.0	0.0	0.0	0.0	0.0	6.5	0.0
<i>Diplothyra smithii</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
<i>Dosinia discus</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Ensis minor</i>	0.0	0.0	0.0	13.3	1.6	1.6	0.0

TABLE 1 – Continued

Percentage of occurrence of different food items in the digestive tracts of selected fishes from Mississippi Sound.

	Species of fish						
	<i>Cynoscion nebulosus</i>	<i>Cynoscion arenarius</i>	<i>Cynoscion nothus</i>	<i>Pogonias cromis</i>	<i>Archosargus probatocephalus</i> Inshore	<i>Archosargus probatocephalus</i> Near islands	<i>Paralichthys lethostigma</i>
Number fish examined	373	108	25	15	77	65	212
Number fish with food	340	74	12	15	63	62	97
Food item	Percentage of occurrence in fish with food item						
<i>Gemma gemma</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Geukensia demissa</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
<i>Ischadium recurvum</i>	0.3	0.0	0.0	33.3	30.2	0.0	0.0
<i>Lyonsia hyalina</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Martesia cuneiformis</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
<i>Mercenaria</i> sp.	0.0	0.0	0.0	0.0	1.6	0.0	0.0
<i>Mulinia lateralis</i>	0.0	0.0	0.0	6.7	6.4	21.0	1.0
<i>Noetia ponderosa</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Nuculana concentrica</i>	0.0	1.4	0.0	0.0	0.0	9.7	0.0
<i>Pandora trilineata</i>	0.0	0.0	0.0	6.7	0.0	9.7	0.0
<i>Semele proficua</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Tagelus plebeius</i>	0.0	0.0	0.0	6.7	0.0	0.0	0.0
<i>Tellina</i> sp.	0.0	0.0	0.0	6.7	0.0	11.3	0.0
Unidentifiable bivalve parts	0.3	0.0	0.0	6.7	6.4	6.5	0.0
Squid							
<i>Lolliguncula brevis</i>	0.3	1.4	0.0	0.0	0.0	1.6	1.0
Barnacles							
<i>Balanus eburneus</i>	0.0	0.0	0.0	0.0	9.5	0.0	0.0
<i>Balanus</i> sp. (unidentifiable)	0.0	0.0	0.0	20.0	17.5	0.0	0.0
Unidentifiable barnacle	0.0	0.0	0.0	6.7	0.0	0.0	0.0
Stomatopod							
<i>Squilla empusa</i>	0.6	2.7	0.0	6.7	3.2	8.1	2.1
Mysidaceans							
<i>Bowmaniella</i> cf. <i>floridana</i>	0.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mysidopsis almyra</i>	1.2	1.4	0.0	0.0	3.2	0.0	6.2
<i>Mysidopsis bahia</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
Cumacean							
<i>Oxyurostylis</i> cf. <i>smithi</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Amphipods							
<i>Ampelisca</i> cf. <i>abdita</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ampelisca</i> sp.	0.9	0.0	0.0	0.0	0.0	3.2	2.1
<i>Ampithoe</i> sp.	0.6	0.0	0.0	0.0	0.0	1.6	0.0
<i>Cerapus benthophilus</i> with tubes	0.0	0.0	0.0	6.7	1.6	0.0	0.0
<i>Cerapus</i> sp. (unidentifiable)	0.3	0.0	0.0	0.0	3.2	0.0	1.0
<i>Corophium lacustre</i>	0.0	0.0	0.0	0.0	14.3	0.0	0.0
<i>Corophium louisianum</i>	0.0	0.0	0.0	13.3	1.6	0.0	0.0
<i>Erichthonius brasiliensis</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>I. epidactylus</i> sp.	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Melita</i> spp.	0.3	0.0	0.0	6.7	1.6	1.6	2.1
<i>Microprotopus</i> cf. <i>raneyi</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Monoculodes</i> sp.	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Paracaprella tenuis</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Unidentifiable amphipod remains	0.6	0.0	0.0	0.0	0.0	1.6	0.0
Unidentifiable haustorid	0.3	0.0	0.0	6.7	0.0	0.0	0.0
Tanaidaceans							
<i>Apseudes</i> sp.	0.6	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 1 - Continued

Percentage of occurrence of different food items in the digestive tracts of selected fishes from Mississippi Sound.

	Species of fish						
	<i>Cynoscion nebulosus</i>	<i>Cynoscion arenarius</i>	<i>Cynoscion nothus</i>	<i>Pogonias cromis</i>	<i>Archosargus probatocephalus</i> Inshore	<i>Archosargus probatocephalus</i> Near islands	<i>Paralichthys lethostigma</i>
Number fish examined	373	108	25	15	77	65	212
Number fish with food	340	74	12	15	63	62	97
Food item	Percentage of occurrence in fish with food item						
<i>Hargeria rapax</i>	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Isopods							
<i>Aegathoa</i> sp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Erichsonella attenuata</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Lironeca ovalis</i>	0.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mothocya nana</i>	0.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nerocila acuminata</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Olencira praegustator</i>	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Penaeids							
<i>Penaeus aztecus</i>	7.4	10.8	0.0	13.3	1.6	1.6	6.2
<i>Penaeus duorarum</i>	0.9	0.0	0.0	0.0	0.0	4.8	0.0
<i>Penaeus setiferus</i>	3.8	8.1	0.0	6.7	3.2	0.0	11.3
<i>Penaeus</i> (unidentifiable remains)	7.1	32.4	25.0	13.3	12.7	8.1	5.2
<i>Sicyonia dorsalis</i>	0.0	0.0	0.0	0.0	1.6	3.2	1.0
<i>Trachypenaeus constrictus</i>	0.0	0.0	8.3	0.0	0.0	3.2	0.0
<i>Trachypenaeus similis</i>	0.6	1.4	8.3	0.0	0.0	17.7	7.2
<i>Trachypenaeus</i> (unidentifiable remains)	0.9	0.0	0.0	0.0	0.0	0.0	1.0
Sergestid							
<i>Acetes americanus</i>	0.0	1.4	8.3	0.0	0.0	1.6	0.0
Carideans							
<i>Alpheus floridanus</i>	0.0	1.4	0.0	0.0	0.0	0.0	0.0
<i>Alpheus heterochaelis</i>	0.0	0.0	0.0	0.0	0.0	6.5	1.0
<i>Alpheus normanni</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Alpheus</i> (unidentifiable remains)	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Latreutes parvulus</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Ogyrides alphaerostis sensu</i> Williams, 1981	0.0	1.4	0.0	0.0	0.0	4.8	0.0
<i>Palaemonetes pugio</i>	3.5	4.1	0.0	6.7	1.6	1.6	1.0
<i>Palaemonetes vulgaris</i>	0.6	0.0	0.0	6.7	1.6	0.0	1.0
<i>Palaemonetes</i> (unidentifiable remains)	0.0	0.0	0.0	0.0	3.2	0.0	0.0
<i>Processa</i> cf. <i>hemphilli</i>	0.0	0.0	0.0	0.0	0.0	4.8	0.0
<i>Tozeuma carolinensis</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Unidentifiable caridean	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Anomurans							
<i>Callinassa jamaicense</i>	1.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euceramus praelongus</i>	0.0	0.0	0.0	13.3	0.0	4.8	0.0
<i>Pagurus longicarpus</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Pagurus pollicaris</i>	0.0	0.0	0.0	0.0	1.6	3.2	0.0
<i>Polyonyx gibbesi</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Upogebia affinis</i>	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Brachyurans							
<i>Callinectes</i> remains	0.9	0.0	0.0	6.7	0.0	11.3	0.0
<i>Callinectes sapidus</i>	8.8	5.4	0.0	13.3	9.5	1.6	2.1
<i>Callinectes similis</i>	0.9	0.0	0.0	0.0	1.6	3.2	0.0
<i>Eurypanopeus depressus</i>	0.0	0.0	0.0	0.0	6.4	0.0	0.0

TABLE 1 – Continued

Percentage of occurrence of different food items in the digestive tracts of selected fishes from Mississippi Sound.

	Species of fish						
	<i>Cynoscion nebulosus</i>	<i>Cynoscion arenarius</i>	<i>Cynoscion nothus</i>	<i>Pogonias cromis</i>	<i>Archosargus probatocephalus</i> Inshore	<i>Archosargus probatocephalus</i> Near islands	<i>Paralichthys lethostigma</i>
Number fish examined	373	108	25	15	77	65	212
Number fish with food	340	74	12	15	63	62	97
Food item	Percentage of occurrence in fish with food item						
<i>Hepatus epheliticus</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Heterocrypta granulata</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Hexapanopeus angustifrons</i>	0.0	0.0	0.0	0.0	0.0	11.3	0.0
<i>Libinia dubia</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Libinia</i> (unidentifiable juvenile)	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Neopanope texana</i>	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Ovalipes floridanus</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Panopeus herbstii</i>	0.0	0.0	0.0	6.7	1.6	0.0	0.0
<i>Persephona aquilonaris</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Persephona punctata</i>	0.0	0.0	0.0	0.0	0.0	1.6	0.0
<i>Pinnixa</i> cf. <i>chaetopterana</i>	0.0	0.0	0.0	0.0	0.0	4.8	0.0
<i>Pinnixa</i> sp.	0.0	1.4	0.0	0.0	0.0	0.0	0.0
<i>Portunus gibbesii</i>	0.3	0.0	0.0	0.0	0.0	1.6	0.0
<i>Portunus</i> cf. <i>spinimanus</i>	0.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Rhithropanopeus harrisi</i>	0.0	0.0	0.0	0.0	3.2	0.0	0.0
Megalops (unidentified)	0.0	0.0	0.0	0.0	3.2	0.0	0.0
Unidentifiable brachyuran larva	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Unidentifiable goneplacid	0.3	0.0	0.0	0.0	0.0	1.6	0.0
Unidentifiable xanthid	0.0	0.0	0.0	20.0	3.2	3.2	0.0
Ectoprocts							
<i>Alcyonidium</i> sp.	0.0	0.0	0.0	0.0	3.2	0.0	0.0
<i>Bugula neritina</i>	0.0	0.0	0.0	0.0	0.0	4.8	0.0
<i>Membranipora arborescens</i>	0.0	0.0	0.0	0.0	1.6	4.8	0.0
<i>Membranipora</i> sp. (unidentifiable remains)	0.0	0.0	0.0	0.0	25.4	0.0	0.0
<i>Zoobotryon verticillatum</i>	0.0	0.0	0.0	0.0	1.6	0.0	0.0
Unidentifiable entoproct colonies	0.0	0.0	0.0	0.0	12.7	0.0	0.0
Echinoderms							
Echinoid (unidentifiable remains)	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Holothuroidea (unidentifiable)	0.0	0.0	0.0	0.0	0.0	3.2	0.0
<i>Hemipholis elongata</i>	0.0	0.0	0.0	0.0	1.6	24.2	0.0
<i>Luidia clathrata</i>	0.0	0.0	0.0	0.0	0.0	8.1	0.0
<i>Mellita quinquesperforata</i>	0.0	0.0	0.0	6.7	0.0	3.2	0.0
Ophiuroid (unidentifiable remains)	0.0	0.0	0.0	0.0	3.2	4.8	0.0
Tunicate							
<i>Molgula manhattensis</i>	0.0	0.0	0.0	6.7	4.8	12.9	0.0
Hemichordate							
<i>Branchiostoma</i> cf. <i>caribaeum</i>	0.6	0.0	0.0	6.7	0.0	0.0	0.0
Fishes							
<i>Anchoa hepsetus</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Anchoa mitchilli</i>	14.4	13.5	0.0	0.0	1.6	21.0	17.5
<i>Anchoa</i> sp.	0.0	0.0	0.0	0.0	0.0	3.2	3.1
<i>Arius felis</i>	0.0	0.0	0.0	0.0	0.0	0.0	2.1

TABLE 1 - Continued

Percentage of occurrence of different food items in the digestive tracts of selected fishes from Mississippi Sound.

	Species of fish						
	<i>Cynoscion nebulosus</i>	<i>Cynoscion arenarius</i>	<i>Cynoscion nothus</i>	<i>Pogonias cromis</i>	<i>Archosargus probatocephalus</i> Inshore	<i>Archosargus probatocephalus</i> Near islands	<i>Paralichthys lethostigma</i>
Number fish examined	373	108	25	15	77	65	212
Number fish with food	340	74	12	15	63	62	97
Food item	Percentage of occurrence in fish with food item						
<i>Brevoortia patronus</i>	11.8	2.7	0.0	0.0	0.0	0.0	0.0
<i>Chloroscombrus chrysurus</i>	0.9	0.0	0.0	0.0	0.0	1.6	0.0
<i>Cynoscion arenarius</i>	1.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cynoscion</i> sp.	0.0	0.0	0.0	0.0	1.6	0.0	2.1
<i>Cyprinodon variegatus</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Dorosoma petenense</i>	1.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Etropus crossotus</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Fundulus similis</i>	0.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gobionellus hastata</i>	0.0	1.4	0.0	0.0	0.0	0.0	0.0
<i>Gobiosoma boscii</i>	1.2	0.0	0.0	13.3	0.0	0.0	0.0
<i>Harengula jaguana</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lagodon rhomboides</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Leiostomus xanthurus</i>	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Membras martinica</i>	3.8	0.0	0.0	0.0	0.0	0.0	0.0
<i>Menidia beryllina</i>	0.6	0.0	0.0	0.0	0.0	0.0	1.0
<i>Micropogonias undulatus</i>	2.9	0.0	8.3	0.0	1.6	0.0	2.1
<i>Mugil cephalus</i>	1.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Myrophis punctatus</i>	0.3	0.0	0.0	6.7	0.0	0.0	0.0
<i>Sphoeroides</i> sp.	0.0	1.4	0.0	0.0	0.0	0.0	0.0
<i>Symphurus plagiosa</i>	0.6	0.0	0.0	0.0	0.0	0.0	1.0
Assumed bait	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Unidentifiable fish parts	38.8	37.8	66.7	0.0	6.4	3.2	53.6
Unidentifiable goby	0.0	1.4	8.3	6.7	0.0	0.0	0.0
Plants							
Detritus (may include some animal matter)	7.4	2.7	0.0	13.3	15.9	4.8	5.2
Filamentous algae	0.0	0.0	0.0	0.0	1.6	1.6	0.0
Unidentifiable plant matter	2.1	0.0	0.0	6.7	9.5	6.5	0.0
Unidentifiable animal remains	0.0	2.7	16.7	0.0	0.0	1.6	0.0
Manmade products	0.3	0.0	0.0	0.0	0.0	0.0	0.0

including passes to the Gulf of Mexico (Table 1), by length of fish sampled (Table 4), and by season in which fish were collected (Table 5). Feeding heavily on a variety of food items, the sheepshead most often contained crustaceans and molluscs. Polychaetes also occurred abundantly in the sheepshead's diet except during summer.

Stomachs of *Paralichthys lethostigma* most frequently contained ingested fishes (Table 6). About one third of the examined southern flounder had penaeid shrimps in their stomachs from spring through autumn, and in winter, when the frequency of penaeids was relatively low, the percentage with mysidaceans in their diet was high.

DISCUSSION

Cynoscion spp.

Cynoscion nebulosus contained a greater variety of food items (at least 60) than did *C. arenarius* (about 20, Table 1). We, however, examined 4.6 times as many fed individuals of the former. The slightly higher prevalence of fish and lower prevalence of crustaceans in the digestive tract of the spotted seatrout compared to those for the sand seatrout (Table 3) may have resulted from greater accessibility to menhaden and specific other fishes by the former shortly before being sampled. *Cynoscion nothus* rarely occurred in Mississippi Sound, but when it was collected,

TABLE 2.

Percentage of occurrence of general dietary groups in fed seatrouts of different lengths in Mississippi Sound.

	<i>Cynoscion nebulosus</i> Length of fish in mm SL				<i>Cynoscion arenarius</i> Length of fish in mm SL			<i>Cynoscion nothus</i> Length of fish in mm SL		
	73-249	250-399	400-532	Total	59-249	250-320	Total	197-249	250-324	Total
Number of fish without food	11	19	3	33	26	8	34	3	10	13
Number of fish with food	100	224	16	340	60	14	74	5	7	12
Food items	Percentage of Occurrence									
Polychaetes	2.0	9.8	6.3	7.4	0.0	0.0	0.0	0.0	0.0	0.0
Molluscs	2.0	1.3	0.0	1.5	0.0	7.1	1.4	0.0	0.0	0.0
Crustaceans	47.0	34.4	31.3	37.9	55.0	71.4	58.1	0.0	71.4	41.7
Fishes	65.0	76.3	75.0	72.9	55.0	57.1	55.4	80.0	71.4	75.0
Other animals	1.0	0.9	6.3	1.2	1.7	7.1	2.7	0.0	0.0	0.0
Detritus	3.0	6.7	18.8	6.2	6.7	7.1	6.8	20.0	14.3	16.7

its stomach content of fishes and crustaceans was similar to that for *C. nebulosus*. Crustaceans in the diet of all three seatrouts consisted primarily of penaeid shrimps. Of those ingested fish that could be identified, *Anchoa mitchilli* and *Brevoortia patronus* were most prevalent. Most fishes had been digested beyond recognition.

As specimens of *Cynoscion nebulosus* from Mississippi Sound grew longer than 25 cm, the percentage of individuals that recently fed on fish increased slightly, concurrent with a slight decrease in frequency of crustaceans eaten (Table 2). The amount of "detritus" increased with length of fish.

The food contents of *C. nebulosus* obtained seasonally included a slightly greater percentage of fish during spring and summer than during autumn and winter, seasons when *A. mitchilli* was more common both in seatrout stomachs (Table 3) and in Mississippi Sound (Perry and Boyes 1978). Penaeids were less prevalent during autumn and winter when they were also less available in Mississippi Sound. During winter, however, the relative frequency of ingested polychaetes and crustaceans other than penaeids was notably high. The use of polychaetes as food during this period was especially notable in large *C. nebulosus*. Unlike seatrouts from some other regions and some other fishes in Mississippi Sound, seatrouts in Mississippi Sound fed throughout the year, albeit probably less so when spawning.

Similar to our findings, those of some other authors also showed that *C. nebulosus* from a variety of localities contained more fish than shrimp, but the percentages of those two prey-groups differed widely (e.g., Eigenmann 1901, Hildebrand and Schroeder 1928, Gunter 1945, Reid 1954, Breuer 1957, Darnell 1958, Miles 1949, Klima and Tabb 1959, Inglis 1959, Tabb 1961 and 1966, Lorio and Schaefer 1966, Fontenot and Rogillio 1970, Carr and Adams 1973, Day et al. 1973, Mahood 1975, Burgess 1976). In fact,

Simmons (1957) found that of 200 fish longer than 500 mm TL in the upper Laguna Madre, Texas, 182 consumed mullet, 12 ate ladyfish, and 6 ate small trout. He noted that "on several occasions mullet 14 inches long were found partially ingested by trout only 21 inches long." He also noted that in a "landcut," trout preferred *Cyprinodon variegatus*. On the other hand, shrimps (usually penaeids) were more frequent than fishes in other collections (Pearson 1929, Baughman 1949, Knapp 1950, Kemp 1949, Miles 1950, Springer and Woodburn 1960, Stewart 1961, Diener et al. 1974). The frequency depended on the season (e.g., Gunter [1945] and Lorio and Schaefer [1966] noted a preference for shrimp in summer, and Moody [1950] noted a maximum of fish in autumn and winter and a maximum of crustaceans in spring and summer even though ingested fish were just as prevalent during spring and summer) as well as the locality and size of seatrout (e.g., Moody [1950] noted penaeids predominating in 150- to 275-mm-SL specimens, and fish, especially *Lagodon rhomboides*, predominating in larger fish). In any event, a notable relationship exists among commercial shrimps, commercial fishes, and seatrouts.

Food for seatrout less than 50 mm long also varies. Copepods make up most of the diet in some localities (Moody 1950, Darnell 1958). Mysidaceans, amphipods, chironomid larvae, carideans, and fishes, however, compose equally or more important prey items in other localities (Reid 1954, Tabb 1961, Odum and Heald 1972, Carr and Adams 1973). In saltwater ponds in Texas, individuals less than 25 mm TL fed primarily on copepods, whereas fingerlings fed primarily on polychaetes, but also abundantly on palaemonid shrimp, amphipods, aquatic insects, and fish (Colura et al. 1976). Quality of diet influences growth in those fish. Taniguchi (1978) documented better growth of

TABLE 3.
Prevalence of *Cynoscion nebulosus* from Mississippi Sound
fed on various dietary groups relative to season

	Season				Total
	Winter	Spring	Summer	Autumn	
Number of fish examined	53	129	104	87	373
Number of fish with food	47	118	90	85	340
Food items	Percentage of occurrence				
Polychaetes	17.0	8.5	2.2	5.9	7.4
Molluscs	0.0	1.7	0.0	3.5	1.5
Penaeids	14.9	17.8	30.0	15.3	20.0
Palaemonids	4.3	1.7	7.8	4.7	4.4
<i>Callinectes</i> spp.	6.4	7.6	14.4	11.8	10.3
Other crustaceans	27.7	9.3	12.2	17.6	14.7
<i>Anchoa mitchilli</i>	19.1	2.5	13.3	30.6	14.7
Other fishes	44.7	79.7	64.4	42.4	61.5
Other animals	0.0	0.0	0.0	4.7	1.2
Detritus	12.8	5.9	4.4	4.7	6.2

larval seatrout when fed on wild copepods as compared to being fed on the laboratory-reared rotifer *Brachionus plicatilis*. Arnold et al. (1976) had used that rotifer followed by a diet of algal-fed artemia to obtain 30% survival at 30 days.

Literature reporting the food of *C. nothus* is lacking, and that for *C. arenarius* is more scarce than that for *C. nebulosus*. Nevertheless, Reid (1954, 1955), Reid et al. (1956), Darnell (1958), Springer and Woodburn (1960), Sheridan and Livingston (1979), and Sheridan (1979) all found that fish was the most abundant item in the diet of *C. arenarius*. Reid et al. (1956) stated that 8 of 15 seatrout longer than 100 mm from East Bay, Texas, had just fed on the Gulf menhaden. Hildebrand (1954) noted both fish and shrimp in the noneverted trout stomach in Texas, and Day et al. (1973) and Diener et al. (1974) found crustaceans, but not necessarily penaeids, important in this species of seatrout from Louisiana and Texas. Darnell (1958) and Inglis (1959) observed mysidaceans and other decapods commonly in fish shorter than 10 cm in other areas of Louisiana and Texas. The most comprehensive feeding study on *C. arenarius* dealt with 79% of 1,545 individuals from Apalachicola Bay, Florida (Sheridan and Livingston 1979, Sheridan 1979). Of those, 62% fed on fishes, primarily *A. mitchilli*, and 26% on mysidaceans, primarily *Mysidopsis bahia*. That mysid plus calanoid copepods constituted the principal diet of individuals smaller than 40 mm long, but the amount gradually tapered off as the seatrout grew and as fish in the diet increased in importance. Diets differed some according to location and season. Also, Sheridan and

Livingston (1979) found that fish were consumed heavily near passes of the estuary, whereas mysidaceans were eaten primarily in the low-salinity East Bay. Sheridan (1978) and Sheridan and Livingston (1979) considered *A. mitchilli* the only planktivore of consequence in the Apalachicola estuary during summer and autumn. They suggested that *C. arenarius* effectively kept the anchovy from utilizing the summer zooplankton peak by feeding heavily on that fish during that season. In Mississippi Sound, numerous fishes other than those discussed in our report feed heavily on *A. mitchilli*. To mention a few, they include *Trichurus lepturus*, *Strongylura marina*, *Bairdiella chrysura*, and probably *Sciaenops ocellata* (see Overstreet and Heard 1978a) and *Micropogonias undulatus* (see Overstreet and Heard 1978b). The squid *Lolliguncula brevis* also serves in that same capacity (Overstreet and Hochberg 1975:898). Near the barrier islands, *Scomberomorus maculatus*, *Synodus foetens*, *Elops saurus*, and other fishes feed heavily on anchovies.

Pogonias cromis

Only 15 specimens of the black drum were examined. Data in Table 1 for those few fish reveal that at least 30 items were consumed with no single item predominating. Of those items, however, 14 were crustaceans and 8 were bivalves.

Because of the drum's ability to crush oysters and other heavily shelled organisms with its pharyngeal teeth, it has been suspected and sometimes identified as destructive to oyster reefs. Most susceptible are single planted oysters, especially those weakened by burrowing pests. Accounts or comments on the drum's destructiveness have been cited by Moore (1899), Goode (1903), Smith (1907), Welsh and Breder (1924), Schlesselman (1955), Hofstetter (1965, 1977), Fontenot and Rogillio (1970), and others. Cave (1978) observed a captive 87-cm-long drum which ate 22 oysters (4 to 6 cm long) per day for a week and a 93-cm specimen which consumed 42 oysters (5 to 8 cm long) per day for the same period. Based on few specimens, he found that captive black drum collected from oyster reefs preferred oysters to other items, whereas drum collected from other habitats preferred *Ensis minor*.

Several other investigators have examined food contents and found molluscs and crustaceans as major food items with polychaetes, fishes, and other items occasionally also listed. These workers include Pearson (1929), Gunter (1945), Kemp (1949), Knapp (1950), Miles (1950), Reid (1955), Breuer (1957), Simmons (1957), Darnell (1958), Simmons and Breuer (1962), and Van Engel and Joseph (1968). Thomas (1971) found the young black drum from tidal creeks of the lower Delaware River in June ate mostly copepods (71%) and chironomids (38%), and in July it ate primarily amphipods (*Corophium* spp., 57%) and chironomids (44%). From August through October *Corophium* spp. made up more than 85% of the diet. In

TABLE 4.

Prevalence of *Archosargus probatocephalus* from Mississippi Sound fed on various dietary groups relative to fish-length

	Length of fish in mm SL		
	145-350	353-449	Total
Number of fish examined	99	43	142
Number of fish with food	86	39	125
Food items	Percentage of occurrence		
Polychaetes	20.9	51.3	30.4
Molluscs	64.0	48.7	59.2
Crustaceans	55.8	71.8	60.8
Fishes	7.0	38.5	16.8
Other animals	51.2	59.0	53.6
Plant	12.8	2.6	9.6
Detritus	10.5	15.4	12.0

other regions, polychaetes or other organisms predominated (e.g., Pearson 1929).

Archosargus probatocephalus

Table 1 shows that the sheepshead has a diverse diet including over 113 species. It apparently even feeds on dead shells to obtain hydroids and other attached fouling organisms. Table 4 shows that a greater percentage of fish from 145 to 350 mm in length fed on molluscs and plants than did larger fish. More than 38% of the large fish contained crustaceans, polychaetes, molluscs, and fishes, whereas only molluscs and crustaceans occurred in that high a percentage of small individuals. Fishes were common only in large sheepshead, and those mostly in spring (Table 5). Even though common in the diet throughout the year, polychaetes occurred most frequently in summer and crustaceans most frequently in spring.

Species of animals in the diet reflected the habitat occupied by the sheepshead. Those fish near the islands contained at least 87 animals compared to 48 from about the same number of examined fish from estuarine habitats. Few prey species occurred in the stomachs of many individuals. Species occurring in more than three fish and indicating a near-island, higher-salinity habitat include *Chaetodipterus variopedatus*, *Dinocardium robustum*, *Nuculana concentrica*, *Pandora trilineata*, *Trachypenaeus similis*, *Hexapanopeus angustifrons*, and *Lucidia clathrata*. In contrast, *Nereis succinea*, *Ischadium recurvum*, *Balanus eburneus*, *Corophium lacustre*, and *Eurypanopeus depressens* were restricted to inshore collections. Some invertebrates such as *Nassarius acutus* and *Mulinia lateralis*, which inhabit sandy-mud areas off Deer Island, and *Molgula manhattensis*,

TABLE 5.

Prevalence of *Archosargus probatocephalus* from Mississippi Sound fed on various dietary groups relative to season

	Season				
	Winter	Spring	Summer	Autumn	Total
Number of fish examined	29	48	37	28	142
Number of fish with food	22	41	34	28	125
Food items	Percentage of occurrence				
Polychaetes	50.0	36.6	8.8	32.1	30.4
Molluscs	59.1	53.7	58.8	67.9	59.2
Crustaceans	59.1	75.6	47.1	57.1	60.8
Fishes	9.1	31.7	2.9	17.9	16.8
Other animals	54.6	41.5	61.8	60.7	53.6
Plants	0.0	4.9	20.6	10.7	9.6
Detritus	9.1	4.9	20.6	14.3	12.0

which colonizes pilings, occurred in the diet of fish from inshore, lower-salinity areas in addition to island locations.

Heavy infestations of parasites that had been present long enough to mature in their hosts, and which had apparently been acquired by the sheepshead from near the islands, indicate that some individual fish collected near the islands had either returned to or never left that general area. Examples include the ascaridoid nematode *Hysterothylacium reliquens* and the aspidogastroid trematode *Cotylogaster basiri* (see Deardorff and Overstreet 1981, Hendrix and Overstreet 1977).

The general feeding behavior of the sheepshead is fairly well understood though only a few studies based on few fish have been conducted; those studies treated a variety of regions. Fish from different regions do feed on different items. Even though not necessarily representative of the particular habits in Mississippi, the behavior documented by Odum and Heald (1972) is worth mentioning. In the Everglades, very small sheepshead lived in grass beds of Florida and Whitewater bays where they fed first on copepods and then on amphipods, chironomids, mysidaceans, and some algae. By the time those fish reached 35 mm, they moved to regions with a harder substratum where they fed on small molluscs and acquired a diversified diet consisting mostly of encrusting forms. In the dry season (January-May) when the water was especially salty, the fish (48 to 267 mm long) fed heavily on the mussel *Brachidontes exustus* and on hydroids. In the wet season when the water was fresher, the diet consisted primarily of the mussel *Congeria leuco-phanta* and the crab *Rhithropanopeus harrisi*.

The sheepshead typically feeds on the bottom, but occasionally uses its sharp incisor teeth to graze off encrusted

TABLE 6.
Prevalence of *Paralichthys lethostigma* from Mississippi Sound
fed on various dietary groups relative to season

	Season				Total
	Winter	Spring	Summer	Autumn	
Number of fish examined	34	72	61	45	212
Number of fish with food	15	40	14	28	97
Mean SL (mm) of fish with food	179	227	235	247	
Range of fish length	125-290	168-359	157-320	150-410	
Food items	Percentage of occurrence				
Polychaetes	0.0	5.0	0.0	0.0	2.1
<i>Lolliguncula brevis</i>	0.0	0.0	7.1	0.0	1.1
Stomatopods	6.7	2.5	0.0	0.0	2.1
Mysids	33.3	0.0	0.0	0.0	5.2
Amphipods	13.3	0.0	14.3	0.0	4.2
Penaeids	20.0	30.0	35.7	39.3	32.0
Palaeomonids	6.7	0.0	0.0	3.6	2.1
<i>Callinectes sapidus</i>	0.0	2.5	0.0	3.6	2.1
Other decapods	0.0	5.0	0.0	0.0	2.1
<i>Anchoa mitchilli</i>	0.0	42.5	0.0	7.1	19.6
Other fishes	60.0	65.0	71.4	50.0	60.9
Detritus	0.0	2.5	7.1	17.9	7.3

items from pilings and other structures. Unlike the superficially similar black drum which has large crushing pharyngeal teeth, it does not feed heavily on oysters. It feeds more on oyster pests such as mussels, crepidulas, barnacles, and crabs. When sea-grasses or algae are plentiful, the sheepshead will occasionally feed heavily on those plants. Even though they are not listed in the tables, we have commonly observed grass balls in 20-cm-long sheepshead in Fort Bayou of Ocean Springs, Mississippi. Vegetation was considered an important dietary item by Darnell (1958) and Fontenot and Rogillio (1970) in fish from Louisiana and by Gunter (1945) and Simmons (1957) in fish from Texas.

The sheepshead depends heavily on crustaceans and molluscs for food in most regions. It additionally feeds on other items, but Mississippi Sound seems to offer a wider range of items than other regions that have been studied. In fact, we suggest that analysis of the sheepshead's diet in particular is a practical procedure to assess prevalence and abundance of numerous species of invertebrates by season and specific habitat. Presumably, based on the large number of different food items and the relatively few specimens of the sheepshead examined, the fish feeds on nearly anything it can get into its mouth. Probably, a few items are avoided (e.g., Prezant 1980).

In addition to the references cited above, Brooks (1894),

Linton (1905), Smith (1907), Hildebrand and Schroeder (1928), Miles (1950), Viosca (1954), Reid et al. (1956), Springer and Woodburn (1960), and Mook (1977) provided some data on food contents. Springer and Woodburn (1960) looked at fish less than 50 mm long in Tampa Bay, Florida, and found them to feed on amphipods, copepods, and polychaetes rather than on molluscs and barnacles like the larger individuals, and Viosca (1954) presented an informative article for someone attracted to sportsfishing for the sheepshead.

Henwood et al. (1978) reported specific dietary items for the related *Stenotomus caprinus* from several localities offshore from the barrier islands where the sheepshead was collected. They noted that the porgy, similarly to the sheepshead in our study, browsed opportunistically on a diverse diet. It, however, fed on fewer molluscan prey than the sheepshead; the invertebrate prey characterized the offshore substratum-types from where the fish were collected.

Paralichthys lethostigma

Tables 1 and 6 show that fishes, primarily *Anchoa mitchilli* at least during spring, and penaeid shrimps comprised primary dietary items of *Paralichthys lethostigma*. Of the specific items, over 20 in number, some differed seasonally (Table 6), but the overall frequency of ingested fishes and shrimps remained roughly the same throughout the year. Mysidaceans were prevalent in the diet during winter only, the period when penaeids were relatively scarce.

Most papers discussing the southern flounder's diet concern data on few specimens. Three extensive ones report findings involving 234, 171, and 343 fish with food in their stomachs. Those treat individuals from Pamlico Sound, North Carolina (Powell and Schwartz 1979); from Barataria Bay, Louisiana (Fox and White 1969); and from Aransas Bay, Texas (Stokes 1977), respectively. Powell and Schwartz (1979) found fishes (mostly anchovies and sciaenids) and crustaceans (mostly the mysidacean *Neomysis americana*) to comprise nearly the entire diet. Similar to that which we noted, fish occurred more frequently in the diet during spring and summer and more frequently in large individuals. In the stomachs of numerous, unrecorded, small specimens of *P. lethostigma* in Mississippi Sound, we noted an abundance of mysidaceans throughout the year. They consisted primarily of *Mysidopsis almyra*. Fox and White (1969) found that fishes, especially the bay anchovy and striped mullet, constituted the major portion of the diet. By volume, 94% of the food items was fish and 6% was crustaceans. Those authors also noted a seasonal change in species-composition: the fish *Dormitator maculatus* was the common food item in autumn, but was absent during the rest of the year. Rather than eating larger items as it increased in length, the flounder ate more individuals of the same size items. Stokes (1977) did not group data seasonally, but flounder 10 to 150 mm TL fed primarily on

mysidaceans and those over 150 mm fed on fishes (primarily *Anchoa* sp., *Mugil* sp., *Brevoortia* sp., and *Micropogonias undulatus*) and *Penaeus* sp. Other workers found different proportions of ingested fish to crustaceans to miscellaneous items, but these proportions probably reflect the availability of those items at the time the specimens were collected (Hildebrand and Schroeder 1928, Gunter 1945, Knapp 1950, Miles 1950, McLane 1948, Kemp 1949, Reid 1954, 1955; Reid et al. 1956, Darnell 1958, Inglis 1959, Diener et al. 1974, and Burgess 1976).

Several factors in addition to those we discuss above influence growth of fishes. A laboratory investigation by Peters and Kjelson (1975) determining feeding and growth rates of small individuals of *P. lethostigma* exemplify this. They found a higher growth rate at 30°C than at lower temperatures. The conversion efficiency depended on salinity concentration; as salinity decreased, the temperature for maximal efficiency increased. This efficiency was greatest when the flounder ate between 70 and 90% of the maximal amount of food offered. This amount, however, decreased with decreasing temperature. Peters and Kjelson (1975) suggested that, no matter what stimulated migration of the

flounder to low-salinity estuarine water in summer and back to high-salinity water in winter, migration placed it in a salinity that maximized growth and conversion efficiency. Stickney and White (1974) also found that fish 0.15 g grew faster for 6 weeks at 5 ppt, but that those 0.50 g grew faster for the same period at 25 ppt. When in the natural environment, the flounder and most other fishes have these factors plus others regulating growth. Some of those factors confined to controlling the feeding rate—in addition to fish size, prey density, temperature, and salinity—include stomach volume, volume of previously consumed food, state of maturation, genetic characteristics, prey species, prey size, time of day, length of day, and moon phase.

ACKNOWLEDGMENTS

We are grateful to the following people for aiding with various aspects of the study: Ronnie Palmer, Kay Richards, Roswitha Buxton, Laurie Toomey, Joan Durfee, Pamela Grimes, Rena Krol, Tom Deardorff, Tom Mattis, Alan Fusco, and Beryl Heard. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

Evaluation of Flow-Through, Static, and Recirculating Systems for the Intensive Culture of the Gulf Killifish *Fundulus grandis* with Observations on a Solar-Heated Recirculating System for the Bait Industry

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DOI: 10.18785/grr.0702.06

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Recommended Citation

Ogle, J. T. and M. A. Solangi. 1982. Evaluation of Flow-Through, Static, and Recirculating Systems for the Intensive Culture of the Gulf Killifish *Fundulus grandis* with Observations on a Solar-Heated Recirculating System for the Bait Industry. Gulf Research Reports 7 (2): 151-156.

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EVALUATION OF FLOW-THROUGH, STATIC, AND RECIRCULATING SYSTEMS FOR THE INTENSIVE CULTURE OF THE GULF KILLIFISH *FUNDULUS GRANDIS* WITH OBSERVATIONS ON A SOLAR-HEATED RECIRCULATING SYSTEM FOR THE BAIT INDUSTRY

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ABSTRACT Three systems (flow-through, static, and recirculating) for intensive culture of the Gulf killifish (*Fundulus grandis*) for bait were evaluated. The outdoor recirculating system proved most successful. Killifish maintained in this system attained an average weight of over 2.0 gm in 42 days, an acceptable market size. Whereas the solar-heated recirculating system sustained fish densities equivalent to 1,000,000/ha and a survival rate of 86%, growth of killifish in this system was less than that observed in both the static and outdoor recirculating systems. Algae appeared to be an important nutritional component of the diet of juvenile killifish. Individuals of *F. grandis* fed diets supplemented with algae grew better than those maintained without them.

INTRODUCTION

The Gulf killifish *Fundulus grandis* Baird and Girard, is used extensively as a live bait along the northern Gulf of Mexico and supports a growing bait industry (McIlwain 1977, Tatum and Helton 1977, Tatum et al. 1978). However, supply of killifish-bait rarely meets the demand, especially during fall when the need is greatest (McIlwain 1977, Tatum et al. 1978). To fill this need, several attempts have been made to propagate killifish. Although the current and predominant method of rearing *F. grandis* is in earthen ponds (see Tatum et al. 1978), McIlwain (1977), based on limited experiments, suggested the feasibility of recirculating systems for killifish culture. Closed recirculating systems, in addition to providing some control over environmental parameters such as temperature, salinity, dissolved oxygen, and pH, require less space and aid in eliminating certain debilitating parasitic infections of killifish (see Solangi and Overstreet 1980, Solangi and Ogle 1981).

This paper reports results of several experiments on killifish culture in closed systems with preliminary observations on a solar-heated recirculating system that shows promise for the bait-fish industry.

MATERIALS AND METHODS

Laboratory-reared *Fundulus grandis* were obtained by stripping gravid male and female killifish collected from Halstead Bayou, Ocean Springs, Mississippi. Prior to experimentation, parasite-free fish were maintained in 60-l aquaria in Instant Ocean® at 25 ‰ salinity and 24 ± 2°C temperature, and were fed daily *ad libitum* a ration of TetraMarin®. Experiments were conducted to compare

flow-through, static, and recirculating systems for killifish culture and determine the effects of various diets on growth of *F. grandis*. Unless otherwise noted, tests were conducted in duplicate, and experimental fish were fed *ad libitum* a ration of Bama® Minnow Chow. Growth was calculated by differences in weight gained, and statistical analyses on growth data were conducted using procedures of Campbell (1967).

Flow-through System

Growth and survival of killifish in an outdoor flow-through system was studied. Two 4000-l circular tanks, 2.5 m in diameter, (Fig. 1a) were filled with seawater from Biloxi Bay. Ambient bay water was pumped through the flow-through tank at a rate of 12 l/min. Overflowing water was removed through a slotted standpipe and venturi arrangement. Salinity and temperature of the Bay water ranged from 1 to 14 ‰ and 22 to 30°C, respectively. Juvenile killifish at the beginning of the experiment were 30 days old and weighed an average of 11 ± 1 (S.E.) mg. Five hundred fish were introduced into each of the flow-through tanks. At the end of the experiment all surviving fish were counted and measured.

Static System

This experiment was conducted to study growth and survival of killifish reared in outdoor static tanks. Two tanks (Fig. 1b), each a rectangular box (1.8x3.6 m) constructed of wood, lined with plastic, and without the filters as indicated in the figure, were filled with approximately 3,300 l of seawater at 20 ‰ which was not exchanged during the 58-day experimental period. Killifish at the beginning of the experiment were 45 days old and averaged 149 ± 26 (S.E.) mg.

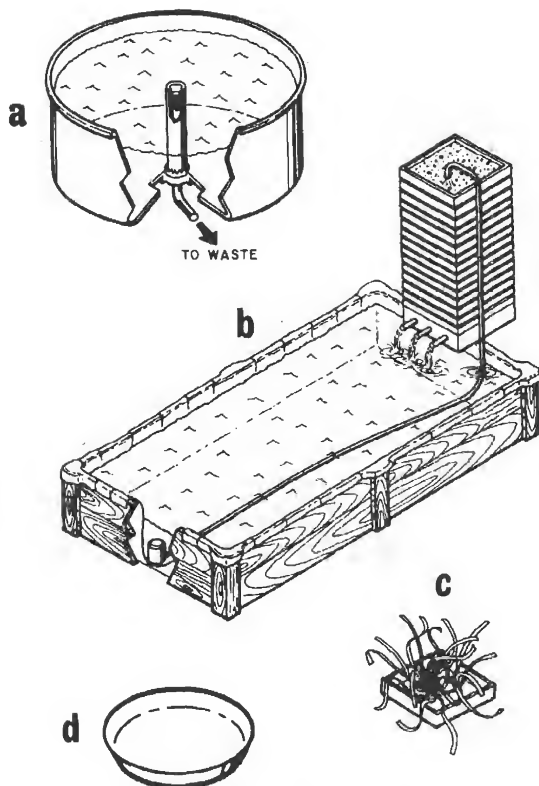


Figure 1 (a-d). Various containers used in experimental studies on killifish.

In addition to the aforementioned two tanks, a third static tank was used to observe the effect of algae in the system on growth and survival of killifish. The tank was filled with approximately 3,300 l of seawater at 20 ‰ and, after the addition of 165 killifish, fertilized with about 200 g of cottonseed meal to initiate a phytoplankton bloom. Fish at the beginning of the experiment were 45 days old and weighed an average of 149 ± 26 (S.E.) mg. Seawater was not exchanged during the 72-day experiment; all surviving fish were counted and measured. This test was not run concurrently with the previous one.

Recirculating systems

Growth and survival of killifish in two systems, outdoor recirculating tanks and a solar-heated recirculating raceway, were studied.

The two outdoor recirculating tanks (Fig. 1b) were the same tanks used in the static tests, except that now each tank was fitted with a trickle-through filter at one end.

These filters consisted of a stack of 15 perforated plastic trays 58x58 cm packed with styrofoam chips. A submersible 1/8-hp pump with a flow rate of 12 l/min was used to pump seawater to the top of each filter and it was allowed to percolate down the filter before entering the tank. In addition to the filter, one of the tanks received three habitats (additional surface area) each consisting of a plastic tray with approximately 1-m long plastic strips woven through it (Fig. 1c). Both tanks were filled with approximately 3,300 l of seawater at 20 ‰ and stocked with 165 120-day-old fish averaging 764 ± 32 (S.E.) mg. After the fish were introduced into the system, the seawater was fertilized by adding approximately 200 gm of cottonseed meal. The experiment ran for 42 days, at the end of which surviving fish were counted and measured.

The solar-heated recirculating system consisted of a raceway housed in a passive solar-heated greenhouse (Fig. 2). The rectangular raceway, 7.9x1.8x0.6 m, with circular ends had a lengthwise panel holding 28 PVC airlifts each approximately 3.8 cm in diameter. Because of the small size of the fish at stocking and the strong currents produced by the airlifts, the air system was turned on for 1 hour three times a day. Water from the raceway was pumped into a 450-l conical settling tank by means of a submersible pump and then flowed by gravity to updraft trickle-through filter boxes, 1.2x0.6 m, stacked in three banks of three boxes each. Water, after passing through the filters, returned to the raceway at the end opposite to the intake. The entire raceway and all associated filters were housed in an insulated building with a window facing south and inclined at 45° for maximal winter solation. The window could be closed by six insulated panels thereby allowing control over water temperature. The raceway was stocked with 670 30-day-old fish weighing an average of 149 ± 26 (S.E.) mg. The experiment lasted 72 days after which all surviving fish were counted and measured.

Diet

To determine whether algae in the diet affected growth and survival of killifish, we introduced 15 fish, averaging 78 ± 8 (S.E.) mg, into each of the six static circular plastic pools (see Fig. 1d) with approximately 40 l of algal water obtained from a large outdoor algae culture tank. Three duplicated diet regimens were used—no food (control), Purina® Trout Chow, and a mixture of Trout Chow and frozen oysters. To serve as control, 15 fish in each of six additional pools were provided with filtered bay water instead of algal water and were fed the aforementioned diet regimens. Salinity and temperature in each pool remained at 20 ± 2 ‰ and $25 \pm 2^\circ\text{C}$, respectively. The tests were run for 38 days, at which time all surviving fish were counted and measured.

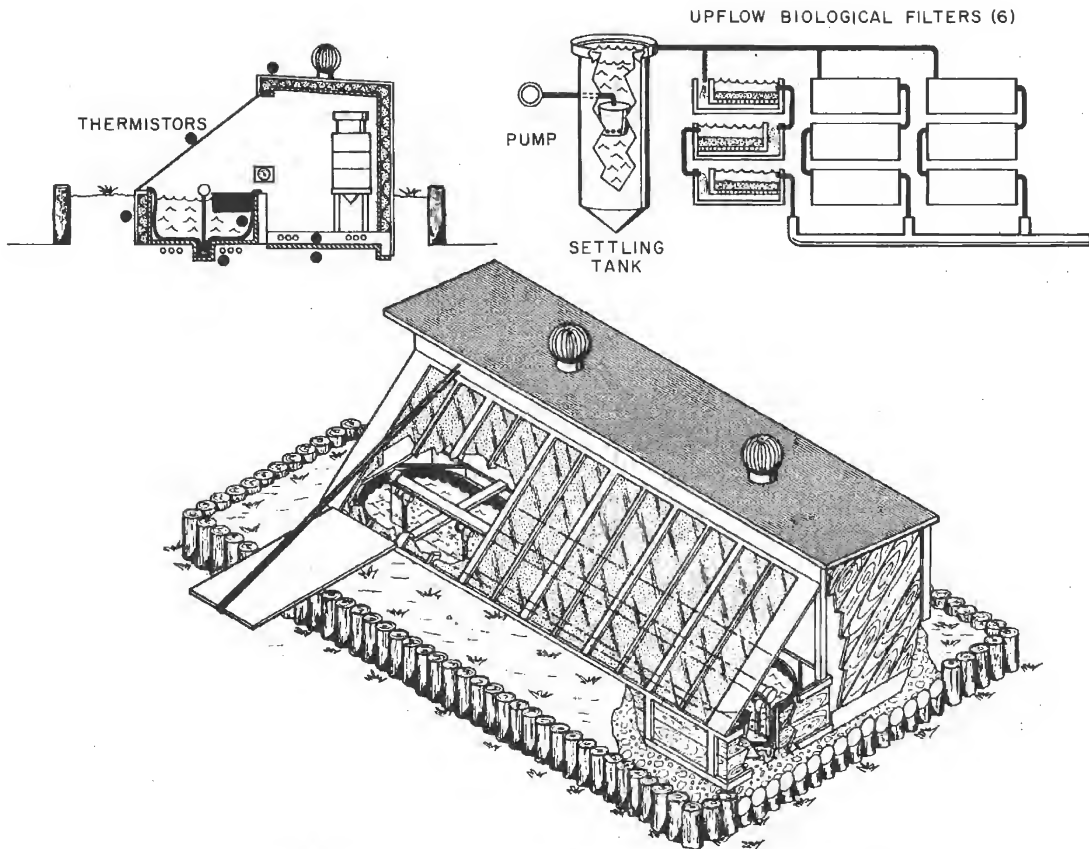


Figure 2. Design of the solar-heated recirculating system used for killifish culture.

RESULTS

Flow-through system (Table 1)

Killifish in tank A grew approximately 92 times their original body weight during the 58-day experiment; however, they did not achieve an acceptable market size (1.5 to 2.0 gm). Fish in tank B did not grow as well as those in tank A, and, in addition, suffered an extremely high rate of mortality (Table 1). No algal blooms were observed in either flow-through tank during the experiment.

Static system (Tables 2 and 3)

Killifish in static tanks A and B (non-fertilized) did not reach a marketable size during the 58-day test (Table 2). However, fish in outdoor static tank C, which was fertilized to promote algal growth and maintained at approximately half the density of the previous test, reached marketable size during the 72-day experiment. Some algae was observed in tanks A and B during the study; however, dense blooms

of mainly unicellular algae were observed in the tank that was fertilized.

Recirculating systems

Outdoor recirculating tanks (Table 4) — Killifish in both tanks exceeded the acceptable market size of 2.0 gm in 42 days. These results, however, are based on a random subsample of 21 individuals from each tank taken on day 42. The reason for this is because the experiment had to be terminated on day 55, when the majority of the fish from both tanks were lost due to an overflow problem. Based on data in table 4, provision of additional surface area (habitat) to tank B did not significantly ($P < .001$) affect growth of killifish. Dense algal blooms were observed in both tanks during the experiment.

Solar-heated raceway (Table 5) — Killifish in this system did not achieve an acceptable market size during the 72-day test. No algal blooms were observed in the raceway throughout the experiment.

TABLE 1.
Growth and survival of killifish after 58 days in an outdoor flow-through system.¹

	TANK A	TANK B
Initial number of fish	500	500
Sample size at harvest	294	64
Average initial weight, mg ($\bar{x} \pm \text{S.E.}$) (N=164)	11 \pm 1	11 \pm 1
Average weight at harvest, mg ($\bar{x} \pm \text{S.E.}$)	1020 \pm 46	180 \pm 10
Weight gain, mg	1009 (93x)	169 (16x)
Survival, %	59	13

¹Experimental period: 25 April to 21 June 1979; stocking density 500,000/ha; initial age of fish: 30 days.

TABLE 2.
Growth and survival of killifish after 58 days in an outdoor static system.¹

	TANK A	TANK B
Initial number of fish	411	457
Sample size at harvest	293	292
Average initial weight, mg ($\bar{x} \pm \text{S.E.}$) (N=164)	11 \pm 1	11 \pm 1
Average weight at harvest, mg ($\bar{x} \pm \text{S.E.}$)	910 \pm 48	560 \pm 30
Weight gain, mg	899 (83x)	549 (51x)
Survival, %	71	63

¹Experimental period: 25 April to 21 June 1979; stocking density 500,000/ha; initial age of fish: 30 days.

TABLE 3.
Growth and survival of killifish after 72 days in an outdoor static tank.¹

	TANK C ²
Initial number of fish	165
Sample size at harvest	148
Average initial weight, mg ($\bar{x} \pm \text{S.E.}$) (N=66)	149 \pm 26
Average weight at harvest, mg ($\bar{x} \pm \text{S.E.}$)	2613 \pm 118
Weight gain, mg	2464 (18x)
Survival, %	90

¹Experimental period: 17 April to 18 June 1980; stocking density 250,000/ha; initial age of fish: 45 days.

²Seawater contained dense cultures of unicellular algae.

TABLE 4.
Growth of killifish after 42 days in outdoor recirculating tanks.¹

	TANK A	TANK B ²
Initial number of fish	165	165
Sample size at harvest	21	21
Average initial weight, mg ($\bar{x} \pm \text{S.E.}$)	764 \pm 32	764 \pm 32
Average weight at harvest, mg ³ ($\bar{x} \pm \text{S.E.}$)	2374 \pm 108	2021 \pm 135
Weight gain, mg	1610 (3x)	1257 (2.6x)

¹Experimental period: 26 June to 6 August 1980; stocking density 250,000/ha; seawater contained dense cultures of algae; initial age of fish: 120 days.

²Tank with additional surface area (habitat).

³No significant ($P < .001$) difference between weights of the two groups (t-Test).

TABLE 5.
Growth and survival of killifish after 72 days in a solar-heated recirculating raceway.¹

	Solar-heated raceway
Initial number of fish	670
Sample size at harvest	572
Average initial weight, mg ($\bar{x} \pm \text{S.E.}$) (N=66)	149 \pm 26
Average weight at harvest, mg ($\bar{x} \pm \text{S.E.}$)	764 \pm 32
Weight gain, mg	615 (5x)
Survival, %	86

¹Experimental period: 17 April to 18 June 1980; stocking density 1,000,000/ha; no algal blooms observed throughout experiment; initial age of fish: 45 days.

Diet

As indicated by data in Table 6, killifish fed diets supplemented with mixed cultures of live algae gained significantly more weight ($P < .05$) than those maintained in filtered seawater. Furthermore, fish fed a mixture of Purina[®] Trout Chow with oyster meat grew significantly larger ($P < .05$) than those killifish fed exclusively on Purina Trout Chow or those not fed during the entire experiment (Table 6).

No detailed analyses were attempted of the species composition of the algal blooms. However, occasional microscopic examination of the algae culture revealed the presence of several unicellular algal species such as *Chlorella*, *Chlamydomonas*, and unidentified diatoms.

DISCUSSION

Based on our observations, very little control over such environmental parameters as temperature and salinity, and

TABLE 6.

Effect of algal water and various diets on growth and survival of killifish maintained in static pools for 38 days.¹

	Bay Water			Algal Water		
	Unfed ²	Trout Chow ³	Mixture ⁴	Unfed ²	Trout Chow ³	Mixture ⁴
Sample size at harvest	13	25	25	19	30	29
Average weight at harvest (mg)	63±1	110±2	170±3	74±7	156±13	253±41
($\bar{x} \pm S.E.$)						
Weight gain, %	-19	41	118	-6	100	224
Average survival, %	43	83	84	63	100	97

¹Stocking rate: 15 fish/tank; Average stocking weight (mg) 78 ± 8 (S.E.); Experimental period: 7 July to 24 August 1980.²No significant ($P < .05$) difference between weights of the two groups. (t-Test)³Significant ($P < .05$) difference between weights of the two groups. (t-Test)⁴Significant ($P < .05$) difference between weights of the two groups. (t-Test)

TABLE 7.

Comparison of average daily weight gain of killifish in flow-through, static, and recirculating systems.

	Stocking density	Average initial weight (mg)	Age at stocking	Average final weight (mg)	Average weight gain (mg/day)
Flow-through system ¹					
Tank A	500,000/ha	11±1	30	1020±46	17.4
Tank B	500,000/ha	11±1	30	180±10	3.0
Static system ²					
Tank A	500,000/ha	11±1	30	910±48	15.5
Tank B	500,000/ha	11±1	30	560±30	9.5
Tank C ³	250,000/ha	149±26	45	2613±118	34.3*
Recirculating systems					
Outdoor recirculating ⁴					
Tank A	250,000/ha	764±32	120	2374±108	38.4*
Tank B	250,000/ha	764±32	120	2021±135	30.0*
Solar-heated recirculating					
Tank A	1,000,000/ha	149±26	45	764±32	8.6**

¹, ², ³, ⁴: Data for Tables 1, 2, 3, and 4 respectively.

*Dense algal cultures present in system throughout the study.

**No algal blooms observed throughout the study.

other water-quality conditions was possible in the flow-through system. Poor growth and high mortality in this system could be attributed to wide fluctuations in temperature and salinity, and possibly to such water-quality parameters as silt in the incoming seawater. Unless methods can be developed to control some of the aforementioned parameters, a flow-through system as described does not appear to be a reliable method for killifish production.

Algae in the diet appear to fulfill some of the nutritional needs of cultured killifish. Fish fed diets supplemented with algae grew better than those maintained without them (see Table 7). Although we did not critically evaluate the amount or type of algae consumed by *F. grandis*, gut analyses of several fish reared in tanks with algae revealed large quan-

ties of organic material composed mainly of detritus, diatoms, unicellular algae, and bacteria. Food content analyses of several *Fundulus* species (*F. heteroclitus*, *F. confluentus*, and *F. luciae*) conducted by Harrington and Harrington (1972), Kneib (1978), and Kneib and Stiven (1978) also show algae and other plant and organic material to be an important component of the diet of killifishes, especially of juveniles in the 29- to 59-mm range during summer and fall (Harrington and Harrington 1972, Kneib and Stiven 1978). However, further analyses of the algal composition in the killifish culture facility to determine its nutritional value, and effect of various algal species on growth of *F. grandis* are needed and should prove rewarding.

In addition to algae in the system, fish densities affected growth of killifish. As indicated by data in Table 7, a density of 250,000 fish/ha appeared sufficient for killifish to achieve an average weight of 2 gm or more within 42 to 72 days. However, since not all experiments were conducted concurrently, variation in average weight gain among killifish at the same or different densities could have been influenced by environmental conditions at the time of each experiment.

Of the three systems examined (static, flow-through, and recirculating), the outdoor recirculating system proved most successful. Killifish in this system achieved marketable size within 42 days of the experiment. However, maintaining optimum water temperature and over-wintering killifish in this system would be a problem. On the other hand, the solar-heated raceway appears to be an attractive alternative to outdoor tanks and could be used in the bait-fish industry. The poor growth in the raceway during this study might be attributed to the lack of algae in the system (see Table 7). This problem can be easily remedied by replacing the up-draft trickle-through filters with a biodisc, and promoting

algal growth in the raceway. Furthermore, in addition to requiring less space and providing the bait farmer control over many environmental parameters, the solar-heated recirculating system can effectively prevent the entry into the system of the grass shrimp *Palaemonetes pugio*, an intermediate host of the pathogenic coccidium *Eimeria funduli* (Solangi and Overstreet 1980, Solangi and Ogle 1981). Preliminary studies by Solangi and Ogle (1981) indicate that this parasite, when present, can considerably affect growth of killifish. Although the solar-heated recirculating system shows promise for culture of killifish, additional studies on the economic feasibility of such a system for the bait-industry, and comparison of currently used methods for killifish culture are essential and should prove valuable to the bait farmer.

ACKNOWLEDGMENTS

Dr. Adrian R. Lawler, Steven Shepard, and William Falls (Gulf Coast Research Laboratory) provided laboratory-reared killifish, Dr. Robin Overstreet commented on the manuscript, and Lucia O'Toole typed the paper.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.07

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Recommended Citation

Heard, R. W. and G. D. Goeke. 1982. The Occurrence of *Lightiella* Jones, 1961 (Crustacea: Cephalocarida) in Mobile Bay, Alabama. *Gulf Research Reports* 7 (2): 157-162.
Retrieved from <http://aquila.usm.edu/gcr/vol7/iss2/7>

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THE OCCURRENCE OF *LIGHTIELLA* JONES, 1961 (CRUSTACEA: CEPHALOCARIDA) IN MOBILE BAY, ALABAMA

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ABSTRACT During July 1979, two adult specimens belonging to the cephalocaridan genus *Lightiella* Jones, 1961 were collected in a box core sample taken at the mouth of Mobile Bay, Alabama. These two specimens were compared to the four described species of *Lightiella*, and found to be most similar to the northeastern Atlantic species of *L. incisa* Gooding, 1963 and *L. floridana* McLaughlin, 1976. Due to a combination of differences in the thoracopodal setation and incisor process of the mandible, the Mobile Bay form cannot at this time be assigned to any of the described species of *Lightiella*. The two Mobile Bay specimens may represent an undescribed species or an ecophenotypic variant of *L. incisa*, but until more specimens from Mobile Bay and adjacent waters are available for study, no conclusions can be made on specific identity of this form. Interpretive problems concerning morphological characters of the Mobile Bay specimens and previously described species of *Lightiella* are briefly discussed.

The subclass Cephalocarida Sanders, 1955, contains four genera represented by nine species known from marine habitats scattered throughout the world (Hessler and Sanders 1973, McLaughlin 1976, Knox and Fenwick 1977). Of the four genera, *Lightiella* Jones, 1961, is the largest with four species, followed by *Sandersiella* Shiino, 1965, with three species. The type genus for the subclass *Hutchinsoniella* Sanders, 1955, and the most recently described genus, *Chiltoniella* Knox and Fenwick, 1977, are both monotypic. The species of *Lightiella* occur in both the Atlantic and Pacific Oceans. *Lightiella incisa* Gooding, 1963, and *L. floridana* McLaughlin, 1976 are northwestern Atlantic forms known from the Caribbean and eastern Gulf of Mexico (Gooding 1963, Sanders and Hessler 1964, McLaughlin 1976, Saloman 1978, Stoner 1981). The other two species, *L. serendipita* Jones, 1961, and *L. monniotae* Cals and Delamare Deboutteville, 1970, were described from the Pacific, San Francisco Bay, and New Caledonia, respectively (Jones 1961, Cals and Delamare Deboutteville 1970).

The two specimens of *Lightiella* on which this report is based were collected on 6 July 1979 from a tidal pass at the mouth (south end) of Mobile Bay, Alabama, 2.5 km east of Fort Gaines (30°15'13"N. 88°3'8"W.) from 5.0 m in depth. Hydrographic measurements at time of collection included temperature (29.7°C), salinity (26.9‰), and D.O. (4.5 ppm). The benthic community at this site represents a transitional fauna between that of coarse sands and fine sand-silt-clay substrata. Sediments characteristic of this station are moderately sorted (medium well sorted to coarse) sands with moderate amounts (10-15%) of silt and clay. The dominant polychaete species at this site were *Magelona* cf. *cincta* Ehlers, 1908, and *Malacoceros vanderhorsti*

(Augener, 1927) with seasonal peaks in *Mediomastus* spp., *Myriochele oculata* Zars, 1923, and the archiannelid *Polygordius* sp. Additional invertebrates common at the sampling site were the bivalve *Mulinia lateralis* (Say, 1822), the brittle stars *Micropholis atra* (Stimpson, 1852) and *Hemipholis elongatus* (Say, 1825) and the cephalochordate *Branchiostoma caribaeum* Sundevall, 1853.

Samples were taken with a box corer that sampled an area of 0.093 m². The sample was initially washed in a flotation step with the suspended material collected on a 0.5-mm mesh sieve. The material was then preserved in a 10% buffered formalin-seawater solution and later transferred to 70% ethyl alcohol for identification. For comparison, specimens of *L. floridana* from the Gulf coast of Florida were examined; a single 2.1-mm specimen from the type locality (Anclote Anchorage) and two specimens (2.4 and 2.6 mm) from the Apalachee Bay series reported by Stoner (1981) were made available to us for study.

Our specimens of *Lightiella* from Mobile Bay superficially both appear to be adults measuring 2.7 and 2.9 mm in length and were slightly damaged (some pseudopods and exopodites of the posterior thoracopods and the long terminal setae of caudal rami were missing). The smaller specimen was dissected and the larger one was left intact in a temporary glycerin slide mount. The dissected remains of the smaller specimen are in the collection of the senior author; the larger specimen has been deposited in the Gulf Coast Research Laboratory Museum, Ocean Springs, Mississippi.

The Mobile Bay specimens appear to be most closely related to *L. incisa*, but also share some characters of *L. floridana*. A comparison of the four described species of *Lightiella* and the Mobile Bay form, with nine different morphological characters, is presented in Table 1. *Lightiella* sp. (Mobile Bay) differs from *L. floridana*, the only cephalocaridan previously known from the Gulf of Mexico, by having (1) an incisor process on the mandible with large

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Manuscript received April 28, 1982; accepted August 25, 1982.

TABLE 1.

Comparison of *Lightiella* sp. from Mobile Bay, Alabama, with the four described species of the genus using nine morphological features (summarized from the literature and this study).

	<i>Lightiella</i> sp. Mobile Bay	<i>L. floridana</i>	<i>L. incisa</i>	<i>L. serendipita</i>	<i>L. monniotae</i>
mandible: teeth on incisor process	medial tooth small	both teeth nearly equal	medial tooth small	medial tooth small	both teeth nearly equal (?)
cephalic shield length to total body length	16%	19%*	12%*	16%*	19%*
pseudopod of maxilla 2: number of marginal seta	4	4-5	5	4	not reported or illustrated
exopodite of maxilla: number of setae on medial margin of proximal segment	3	3	2	1	not reported or illustrated
thoracopods 1-6: number of setae on pseudopods	5	5	5	4	not reported or illustrated
telson: pair of sharp, distal, dorsal processes	present	present	present	absent	not reported
caudal rami: length compared to combined length of telsonic and last abdominal segments	distinctly shorter	approximately equal	distinctly shorter	distinctly shorter	distinctly shorter
thoracopodal exopodites: notch on lateral margin of distal segment	present, weakly developed	absent	present	absent	not reported or illustrated
8th thoracopod: spinose process on pleura	absent	present	absent	absent	present

*based on illustrations from original species descriptions

lateral tooth and small medial tooth or "denticle" (Figs. 1A, 3A), (2) some thoracopodal exopodites with lateral notches (not illustrated), (3) caudal rami distinctly shorter than the combined length of the last two abdominal segments¹ (Fig. 2E), (4) no spinose process on the "pleura" of the last (8th) thoracopod (Figs. 2B, D), (5) more elongate body (Fig. 2A) and (6) relatively shorter head length in relation to total body length. Our two Mobile Bay specimens share all of these characters with *L. incisa*; however, they differ from it in other characters. *Lightiella incisa* has two setae on the medial margin of the first exopodal segment of the maxilla, whereas three setae are present at the same location on the maxilla of the Mobile Bay specimens (Fig. 1C). Although not specifically mentioned in the text, McLaughlin (1976) illustrated (Fig. 2A:596) three setae on the medial margin of the first exopodal segment on the maxilla of *L. floridana*. The pseudopod of the maxilla of *L. incisa* has five plumose marginal setae; whereas, the Mobile Bay specimens have four (Fig. 1C). The number of these setae was reported by McLaughlin (1976) to vary between four and five for *L. floridana*. Another character, which may be unique to the

Mobile Bay form, is the apparent absence of a "short" marginal setae (5th from lateral margin in both *L. floridana* and *L. incisa*), on the distal exopodal segments of both 7th thoracopods of the 2.7-mm specimen (Fig. 1E). Unfortunately the exopodites of the seventh thoracopods are missing on the 2.9-mm specimen. It is possible that the short setae on both the 7th thoracopods could have been broken during handling; however, these "short setae" were not present on the 7th thoracopods of a 2.3-mm specimen of *L. floridana* that we examined from collections made by Stoner (1981) at Apalachee Bay, Florida. The total number of marginal setae on the Apalachee Bay specimens was seven, two less than observed on the Mobile Bay specimens. This difference in setal number (and the absence of a short seta) may be due to the size and molt stage of Apalachee Bay specimens. The meristic characters of the labrum, maxillule, antennule, antenna and other thoracopods of the Alabama specimens fall within the described ranges for *L. incisa* and *L. floridana*. *Lightiella incisa*, *L. floridana*, *L. floridana* reported by Stoner (1981) and the Mobile Bay specimens all have fine teeth on the posteroventral margin of pretelsonic abdominal segments (Fig. 2F).

Based on the morphological variation reported for several cephalocaridan species (Hessler and Sanders 1964, Wakabara 1970, Wakabara and Mizoguchi 1976, McLaughlin 1976, Saloman 1978) which include both *L. incisa* and *L. floridana*,

¹Specimens of *L. floridana* collected by Saloman (1978) in shallow offshore waters near Tampa Bay, Florida, like the Mobile Bay specimens, are reported to have distinctly shorter caudal rami than the type material from Anclote Anchorage. We were unable to obtain any of Saloman's specimens for study.

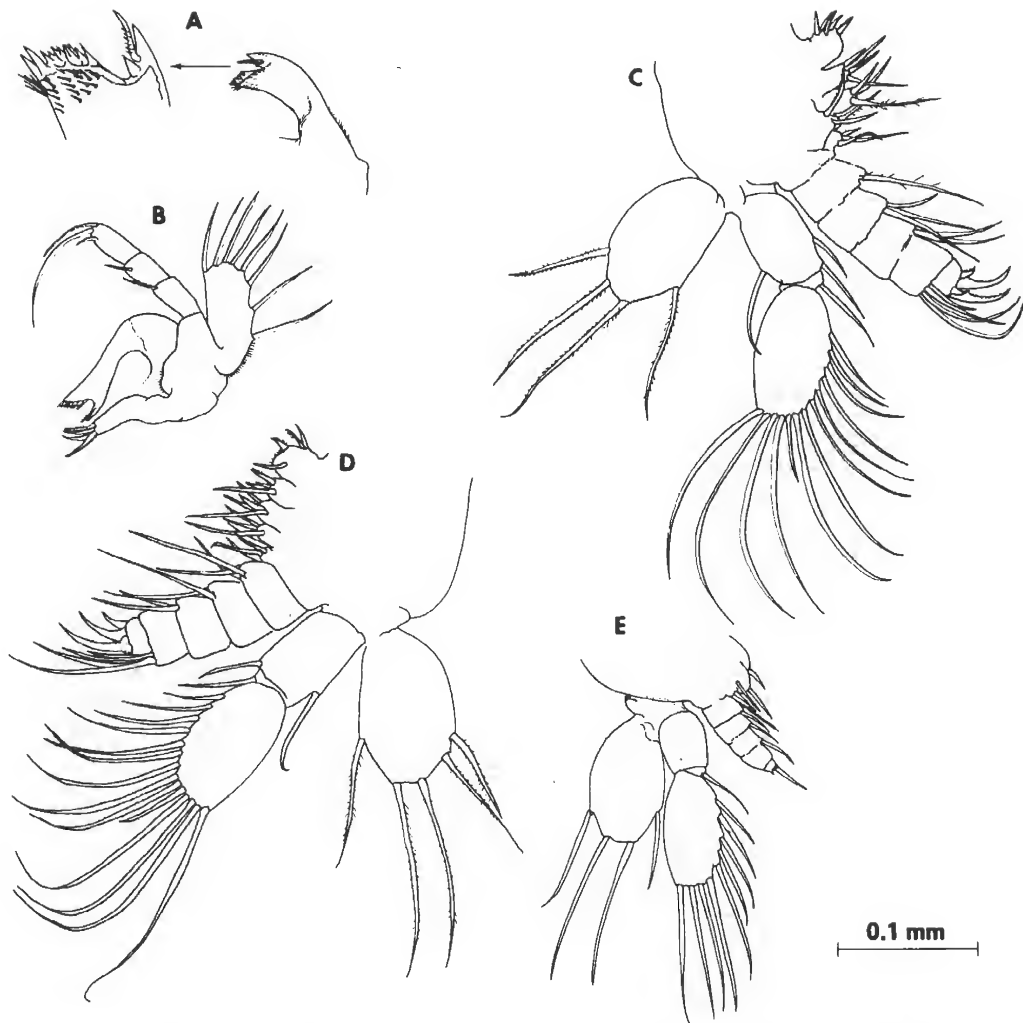


Figure 1. *Lightiella* sp. from Mobile Bay, Alabama (2.7 mm). A, right mandible showing incisor process. B, right mandible and right maxillule. C, right maxilla. D, posterior view of thoracopod 1. E, frontal view of thoracopod 7.

we hesitate to designate a new species based on only two specimens. A larger series of adult and subadult specimens of the "Mobile Bay form" is needed to clarify its specific status. If, based on additional material, the setation differences between our Alabama material and *L. incisa* are found to be consistent, and if the "short" marginal seta indeed does not occur on the exopodite of thoracopod 7, we feel the Mobile Bay form should be named and designated as a new species. Until additional specimens become available for study, we consider our material to be most closely related to *L. floridana* and *L. incisa* and possibly a northern ecotype of the latter species.

Both specimens of *Lightiella* from Mobile Bay were infested with an unidentified and possibly new species of suctorian protozoan. These stalked sessile ciliates occurred primarily along the posterior lateral and posterior ventral margins of the abdominal somites (Fig. 3C), with each somite usually having from one to four specimens. Lighter infestations of a similar or conspecific suctorian were present on the three Florida specimens of *L. floridana* that we examined. The taxonomic status of this protozoan awaits study of living and properly fixed material. This report constitutes the first record of suctorians associated with the Cephalocarida.

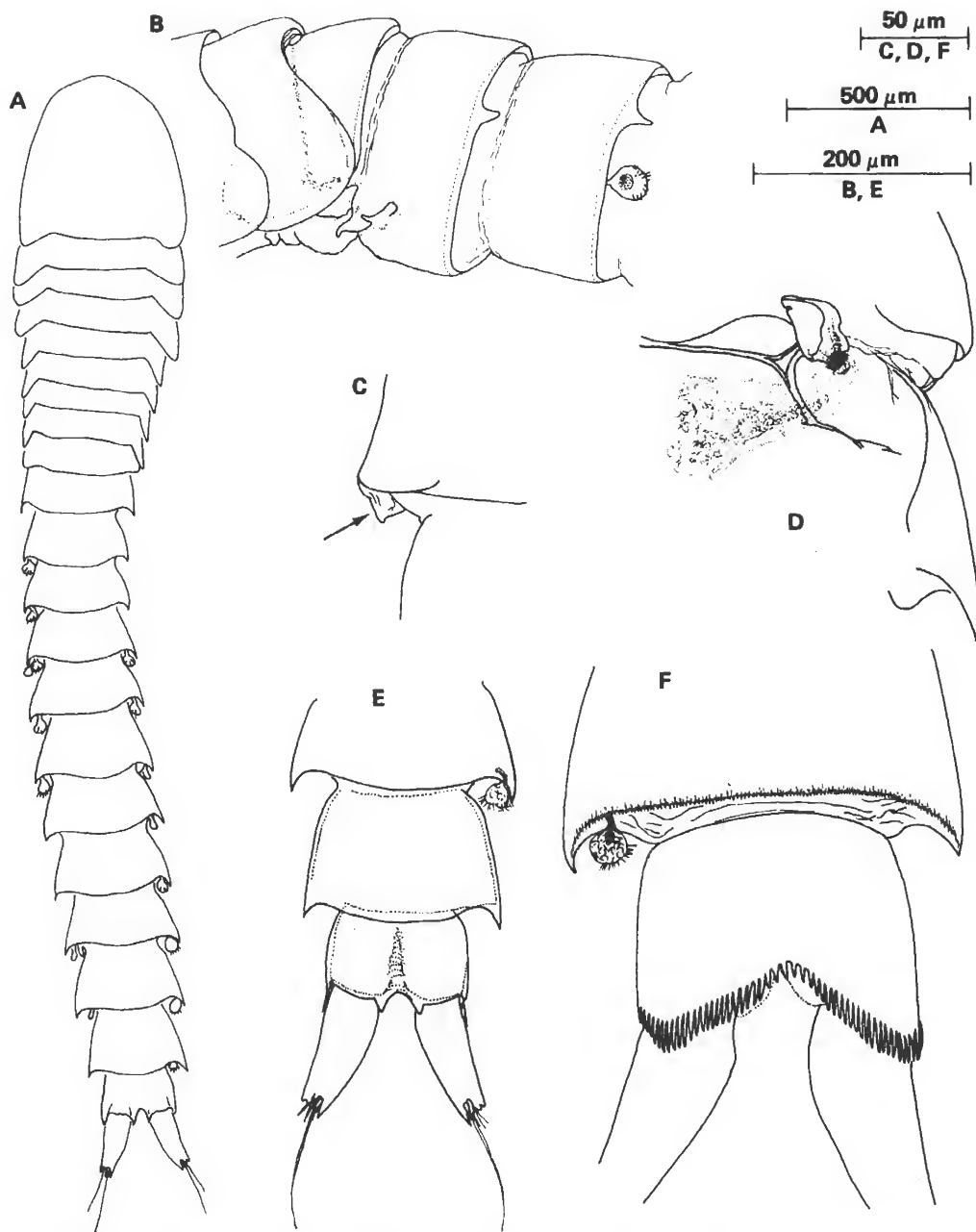


Figure 2. *Lightiella* sp. from Mobile Bay, Alabama (2.9-mm specimen). A, dorsal view of whole specimen. B, lateral view of last three thoracomeres and first two abdominal segments. C, dorsal view of left, lateral, posterior margin of thoracopod 8. D, ventral view of the first thoracomere (left side) showing opening of genital duct. E, dorsal view of last three posterior segments and caudal rami. F, ventral view of abdominal segment 11 and telsonic segment.



Figure 3. A, incisor process (2.7-mm specimen). B, last abdominal segment, telsonic segment and caudal rami (2.7-mm specimen). C, suctorian protozoan attached to base of lateral process of abdominal segment 6 (2.9-mm specimen).

Supplemental comments

During our observation it was noticed that coverslip pressure may cause modification of important taxonomic characteristics. For example, Figure 2C shows an apparent spinose process on the posterior lateral margin of the eighth thoracic segment of the 2.9-mm specimen. This "process" is an artifact resulting from folding of chitin at the posterior margin of the segment while under coverslip pressure. We suggest that specimens should be examined without a coverslip for such characters as the presence or absence of this spinose process and length-width ratio of the somites since they might be altered or distorted by coverslip pressure in temporary or permanent slide preparations.

We had difficulty interpreting the number of segments in the exopods of the thoracopods, especially the maxilla. Jones (1961) in his original description of the type species *L. serendipita*, described four segments in the exopods of the thoracopods. He considered the common base for the exopod and pseudopod and the compressed, wedge-shaped structure, which bears a single medial seta, to be proximal (segment 1) and penultimate (segment 3) segments, respectively. Gooding (1963), however, considered exopodal segments 1 and 3 of Jones' description not to be true segments but "functional subdivisions" of the protopod and the proximal exopodal segment (segment 2 of Jones). This interpretation has been followed by McLaughlin (1976). Based on our observations we agree that segment 1 of Jones (1961) is not a true segment and is part of the protopod; however, the status of segment 3 of Jones (1961) is more difficult for us to interpret. With reservations we have followed Gooding's interpretation in this report, but feel that

the small wedge-shaped structure (penultimate segment of Jones) should be re-examined carefully to check the attachment of the muscles. Based on the limited material available to us, we are unable to draw any definitive conclusions on the status of this structure. It is hoped that investigators having access to living or properly fixed specimens and using tools such as Nomarski optics and carefully prepared histological sections will be able to settle this question.

We should also like to suggest that features of the lateral incisor tooth of *L. serendipita* may have been misinterpreted. Examination of the mandibles of our material and a specimen of *L. floridana* from the type locality, as well as the published descriptions for those of *L. incisa*, *L. monnita* and *L. floridana*, indicate that all of these species have two, simple, unarmed incisor teeth with a serrate or unipectinate spinelike seta arising between them (Figs. 1A, 3A). We noticed in our specimens that the serrate spinelike seta, under certain light conditions and orientations, especially when viewed from ventral aspect, appeared to coalesce or merge with the inner margin of the larger lateral incisor tooth. Under such conditions, the fine serrations on the seta appeared erroneously to arise from the inner margin of the lateral incisor tooth. Jones (1961) did not mention the presence of a serrate seta between the smaller inner and larger lateral incisor teeth of *L. serendipita*; however, he did state that "there are many fine hairs inserted between. . . [these] two teeth." Since *L. serendipita* is the only species of the genus described as having "fine hairs" on its incisor teeth and as lacking a serrate or unipectinate spinelike seta between these teeth, we suggest that its mandible should be re-examined to determine if the "fine hairs" actually may be fine serrations of a previously overlooked seta which is

in close proximity to the lateral incisor tooth. If Jones' (1961) description of the mandible proves correct, we feel the lack of a seta between the incisor teeth and the presence of hairlike seta on these teeth represent important characters that should be taken into consideration in any future systematic or taxonomic treatments of the genus *Lightiella*.

ACKNOWLEDGMENTS

The specimens used in this study were collected during an environmental monitoring program for Mobil Oil South-

east Exploration and Producing, Inc. performed by Tech Con, Inc. The authors gratefully acknowledge James Helis of MOSEPI for his assistance through the duration of the study. We wish to thank Patsy McLaughlin, Florida International University, and Robert W. Virnstein, Harbor Branch Institution, Inc., for loan of specimens. Patsy McLaughlin and Howard Sanders, Woods Hole Oceanographic Institution, read the manuscript and their comments and constructive criticisms were greatly appreciated. Lucia O'Toole and Sharon Wilson typed the drafts of manuscript and Linda Paulson inked Figures 1 and 2.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.08

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Recommended Citation

Gunter, G. 1982. Heat Death of Least Tern Chicks on the Gulfport, Mississippi, Beach in 1980. *Gulf Research Reports* 7 (2): 163-166. Retrieved from <http://aquila.usm.edu/gcr/vol7/iss2/8>

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SHORT COMMUNICATIONS

HEAT DEATH OF LEAST TERN CHICKS ON THE GULFPORT, MISSISSIPPI, BEACH IN 1980

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ABSTRACT The Least Tern is among the smallest of the long-winged flyers and an indescribably ethereal impression emanates from it in flight. Thus great interest was generated when this tern began to nest on the mainland beach of Mississippi Sound about 12 years ago. In 1980, Least Tern chicks died in numbers on the beach and this generated considerable comment and some bombast. An upstate ornithologist announced that poison in the food chain was the cause, but no poison has ever been found in the carcasses of the dead chicks or in the water. The mortality of Least Tern chicks was not caused by Red Tide or disease and by a simple process of exclusion fell to the hottest summer the author ever saw on the Gulf Coast in 51 years, with air temperatures up to 107°F.

INTRODUCTION

The Least Tern, *Sterna albifrons*, appears white in its flight over nesting beaches along the river valleys of North America and the Gulf beaches to Massachusetts, but it has light touches of gray, black and brown. It ranges south to Peru, Brazil, and the Antilles, and north to Scotland, the Baltic and the large rivers of India, China, Japan, Russia, the Caspian Sea, and Africa to Australia. It also nests on various sea beaches and is scattered world wide in that habitat except for the cold zones (Reilly 1968).

It flies in a delicate manner, with its thinly tapered, swept back wings, and there is an indescribably ethereal impression given by these birds as they billow back and forth over their eggs and young. Even such a stern old observer as Oberholser (1973) says, "the Least Tern is extremely bouyant, swift and graceful." Thus, when these fairy-like birds began some 10 years ago to nest on the sand beach of the Mississippi Sound mainland shore within a few yards of U.S. Highway 90, the front thoroughfare of Gulfport, Mississippi, this development aroused the interest of hundreds of people.

Gunter (1957) reviewed the influence of temperate factors on marine organisms. Mammals and birds live at precise body temperatures that cannot vary much. Most poikilotherm organisms live within 4 to 7°F of the upper limit of ambient temperature that they can withstand, while the lower limit may be near freezing, 25°F or lower. For this reason, the trouts and related cold-water fishes in southern Canada and the northern United States sometimes die of heat stroke in natural waters.

The Course of Events

On June 26, 1980, Dr. Jerome C. Jackson found dying Least Tern chicks on the beach at Gulfport, which fact he announced to the local newspaper, *The Daily Herald*, along

with the pronouncement that poison in the food chain was the cause. The writer took issue with that and stated in *The Daily Herald* on July 3 that no poison or pesticide would be found. From that day to this no poison has been reported in the carcasses of Least Tern chicks, although presumably a thorough search was made at Mississippi State University. Six autopsies were made at the Gulf Coast Research Laboratory and no poisons have been found in the waters of Mississippi Sound.

During the late spring and early summer no plankton blooms were seen in Mississippi by the Laboratory staff. These develop sometimes into classical examples of the Red Tide, and some were reported by local fishermen as little as 8 days before the dying terns were reported. For that reason the author suggested to the local newspapers that the Red Tide was a possible cause of death of Least Tern chicks, because of the poisonous anoxines that develop in these instances. However, autopsies of some of the tern chicks carried out at the Gulf Coast Research Laboratory showed no evidence of Red Tide involvement and the idea properly faded into a matter of no importance.

The author had also stated initially that perhaps the baby terns were dying of some viral or bacterial disease, but autopsies of dead tern chicks showed that disease was not involved.

J. G. Mackin, a former head of the Department of Biology of Texas A&M University, discovered several years ago that a rise of a few degrees in temperature caused unrecognized species of bacteria to parasitize the American oyster, *Crassostrea virginica*, in the winter. With these facts in mind, the writer began to suspect that heat was playing a more than normal part in the lives of aquatic animals in the summer of 1980, when Jim Martin's fishing column in *The Daily Herald* reported that all sportfish being taken in the lower Pearl River were covered with fungus.

The Temperature Record

Table 1 gives the official air temperature record for 11

TABLE 1.

Daily air temperature records at Biloxi, Mississippi in °F taken at 3:00 p.m.
for the months of June, July and August from 1970 to 1980, inclusive.

Date	1970			1971			1972			1973			1974			1975		
	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug
1	83	90	91	85	90	78	84	88	87	86	91	90	85	85	90	85	88	81
2	82	96	92	84	87	86	83	89	89	85	92	85	84	87	87	85	90	81
3	85	97	90	87	89	87	87	90	90	87	94	89	86	87	88	86	90	89
4	84	96	90	89	87	88	89	90	95	87	91	89	86	88	86	87	89	82
5	81	88	90	88	89	89	91	89	97	87	91	85	86	88	86	88	95	86
6	83	90	91	88	84	89	92	86	95	86	89	89	87	85	87	90	95	86
7	84	93	91	86	87	90	98	87	94	86	85	89	87	85	86	89	88	85
8	85	94	90	88	89	89	92	89	93	86	90	88	86	87	85	87	99	84
9	85	94	90	88	89	89	87	90	91	87	96	90	87	91	88	85	87	84
10	85	89	91	88	88	89	88	89	92	86	96	91	88	93	89	87	91	85
11	84	87	89	90	89	92	87	90	91	88	97	90	85	93	90	87	90	87
12	87	82	86	90	93	93	86	90	92	87	95	90	86	98	91	83	88	87
13	88	88	88	91	94	92	86	87	92	88	93	85	86	94	90	85	86	89
14	95	89	89	92	92	93	87	88	89	89	87	90	87	89	88	89	88	89
15	91	90	89	92	95	92	87	89	88	90	91	89	87	89	88	86	87	90
16	86	89	86	90	94	94	88	88	89	89	92	85	90	89	88	85	87	90
17	88	89	88	90	90	92	90	89	90	89	94	89	90	89	93	87	82	90
18	93	90	89	88	91	89	92	90	88	90	95	91	86	89	90	89	88	90
19	94	89	88	88	91	90	90	92	95	91	96	91	85	91	92	89	86	90
20	92	90	86	87	90	89	98	89	100	90	90	92	93	94	91	90	90	90
21	91	89	88	90	93	88	98	88	99	89	90	95	90	92	90	88	88	89
22	90	85	90	94	88	89	92	93	94	90	91	94	88	92	87	88	87	87
23	92	87	89	89	87	89	87	90	90	90	96	89	89	91	91	87	88	88
24	88	89	85	86	88	89	91	91	90	93	95	90	88	91	90	87	86	89
25	80	87	87	87	88	87	93	89	90	93	90	92	82	89	88	86	89	89
26	88	88	85	91	89	89	92	89	91	91	89	90	83	87	88	87	91	90
27	90	90	84	88	88	91	92	90	92	90	88	88	84	90	87	87	94	92
28	88	91	83	87	89	91	92	90	92	92	90	92	86	93	88	85	90	92
29	89	91	87	87	89	92	92	91	89	92	92	88	85	93	88	85	85	90
30	88	91	88	87	89	87	89	86	88	92	90	86	85	93	88	86	85	90
31		92	89		81	85		86	87		93	88		90	88		81	89
Avg.	87.3	90.0	88.4	88.5	88.9	89.3	90.0	89.1	91.6	88.9	91.9	89.3	86.6	90.1	88.6	86.9	88.6	87.7

Date	1976			1977			1978			1979			1980		
	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug
1	84	87	94	90	90	92	88	91	92	85	95	91	85	99	92
2	84	88	81	92	94	91	85	96	92	85	90	90	85	94	90
3	85	87	90	92	94	87	82	95	96	86	91	91	86	92	90
4	83	88	89	90	99	85	84	92	99	84	91	92	89	91	91
5	83	85	89	92	89	89	86	92	96	85	95	94	92	92	99
6	80	90	89	94	93	89	86	91	90	87	94	94	91	94	95
7	82	85	91	92	97	90	87	91	89	88	91	93	90	100	96
8	83	85	91	88	98	90	85	90	86	89	90	91	95	94	92
9	89	88	97	88	95	90	88	90	79	89	86	89	96	95	93
10	89	87	94	98	89	88	88	90	82	88	86	92	86	93	91
11	86	86	88	98	89	87	86	88	83	88	83	90	92	97	92
12	90	90	93	94	88	90	91	89	86	85	81	88	94	100	92
13	89	90	92	93	93	89	92	90	87	85	88	88	95	100	93
14	89	91	90	90	96	90	91	90	87	86	90	89	91	100	92
15	87	90	95	90	95	90	88	90	89	86	90	93	89	102	92
16	87	93	95	91	92	88	88	89	90	84	93	92	89	103	90
17	86	92	95	91	91	89	87	93	91	85	93	91	89	96	90
18	86	90	92	90	92	88	86	91	90	86	94	90	93	95	91
19	87	90	91	90	91	88	88	90	91	87	84	89	92	94	92

TABLE 1. (Continued)

Daily air temperature records at Biloxi, Mississippi in °F taken at 3:00 p.m. for the months of June, July and August from 1970 to 1980, inclusive.

Date	1976			1977			1978			1979			1980		
	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug	Jun	Jul	Aug
20	83	89	91	91	90	88	87	90	91	89	87	92	92	89	96
21	87	92	93	92	91	87	88	88	93	91	89	92	89	87	99
22	85	93	91	92	89	87	92	88	92	89	89	92	90	86	99
23	87	93	91	90	92	85	95	89	92	89	88	90	90	96	100
24	87	94	94	91	91	82	96	89	94	90	88	89	90	89	97
25	87	95	95	93	91	87	93	86	92	90	84	88	90	90	92
26	85	95	92	93	90	88	91	90	90	86	88	87	90	87	92
27	84	93	90	91	89	87	92	89	90	88	89	90	87	89	91
28	91	92	80	90	90	87	96	90	90	90	89	90	88	88	90
29	90	91	90	90	91	87	97	88	88	95	90	90	90	89	89
30	87	94	94	90	90	89	96	87	88	NA	91	91	98	95	90
31		92	90		93	89		89	90		91	90		94	92
Avg.	86.1	90.2	91.2	91.5	92.0	88.2	89.3	90.0	89.8	87.4	89.3	90.6	90.4	93.5	92.9

years for the months of June through August. This was the maximum daily temperature and was taken at 3:00 p.m. by Mr. Jerry Knebel of the City of Biloxi. From 1970 through 1979 the mean temperatures for June, July and August were 87.3, 90.0 and 89.5°F. For the year 1980, the means were 90.4, 93.5 and 92.9°F or 3.6% greater than for the previous 10 years. This is an extreme change in long time averages. In view of the great changes on the whole physiological process caused by a few degrees change of body temperature, this could cause a very great change brought by a relatively small environmental change.

Furthermore, between June, July, and August 1970 and 1979 (a period of 920 summer days over 10 years) there was one day only (20 August 1972) when the temperature equaled 100°F. But in 1980 there were 7 days with 100°F or more, with five of them in succession.

On July 26, 1980, the temperature on a bank clock in Ocean Springs, Mississippi, on Highway 90 registered 107°F at 3:00 p.m., which is the highest air temperature the author has seen during 51 years on the Gulf Coast. At that time he remarked that the clock was broken, but it was not. On the same day, *The Daily Herald* reported the air temperature in Gulfport at 106°F and that in Long Beach at 105°F. Considering the distance apart, some 20 to 30 miles down the beach to the west, these temperatures were remarkably similar. This occurred after the deaths of the baby terns were first noted, but it was a continuation of the same hot spell. There is little doubt about the killing heat in the open sand-scapes that constitute the nests of the Least Terns. Table 2 gives the mean temperatures for each month.

During the preceding weeks chickens were dying all over Texas, the midwest and down into Arkansas, and at least 200,000 were reported killed in Mississippi. Following this hot spell there were some cooling rains and the deaths of domestic fowl as well as those of Least Terns came to an end.

Least Terns also nest on Ship Island, Horn Island and Deer Island, the latter being just off the mainland. Some deaths were reported from Deer Island, but none from Horn and Ship and these differences were advanced by a local amateur ornithologist as indication that heat was not the cause of the mortality. However, the sea beaches of Horn and Ship Island, both being offshore barrier islands, are always cooler in the summer than the mainland shore of Mississippi Sound and usually there is a breeze from the sea in the warmer months, which keeps the sea beach cool. To the contrary, cold spells push right to the beach in winter, growing a little warmer as the beach is approached and then the air becomes warmer unless the wind is hard from the north. This regime and the arrangement of sea and land temperatures on the Gulf were explained by Collier and Hedgpeth (1950).

TABLE 2.

Air temperature means by months for the years 1970 through 1980 at Biloxi, Mississippi

	Jun	Jul	Aug
1970	87.3	90.0	88.4
1971	88.5	88.9	89.3
1972	90.0	89.1	91.6
1973	88.9	91.9	89.3
1974	86.6	90.1	88.6
1975	86.9	88.6	87.7
1976	86.1	90.2	91.2
1977	91.5	92.0	88.2
1978	89.3	90.0	89.8
1979	87.4	89.3	90.6
1980	90.4	93.5	92.9
Avg.	87.3	90.0	89.5

The northern Gulf of Mexico coast of the United States is in the cool, wet part of the Carolinian biogeographic zone of the subtropics and as such it experiences cold spells that kill fishes (Gunter 1947, Overstreet 1974) and also heat waves that raise the water temperatures in shore ponds to 35.0°C and a little above (Simpson and Gunter 1956). The meteorologist Reiter (1981) has recently explained the excessively high temperatures of 1980 in the south central states in terms of jet streams influenced by the Rocky and Himalayan Mountains in an article, entitled "The Tibet Connection." He did not mention a single temperature, but there is no doubt of the excess heat. He said, "The 1980 summer heat wave in the south-central United States was marked by a persistent anticyclone in the same area. Meteorologists suspect that this phenomenon was triggered by the Rocky Mountains (which the jet stream tends to cross with an anticyclonic curvature). The anticyclone's persistence was most likely caused by the combined effects of an unchanging pattern of large-scale airflow waves between Tibet and the Rockies, surface temperatures over the Pa-

cific, and feedback from the heat wave itself. The dry and hot soil of the south-central United States acted on the atmosphere as a giant furnace, heating up the lower troposphere and thereby extending the deflecting effects of the Rockies on the tropospheric airflow patterns farther to the east and southeast than is normally the case."

I saw the dying tern chicks one time. They were characterized by neck twisting, which poultry raisers call wry-neck. The medical term is torticollis.

If we may take a broader view, evolutionists are coming to see that the process takes place by beats or jumps with long intervening periods of little change. This fits in with the idea of Taylor (1934) pointing out the increased stress brought about by years of extreme range in environmental factors, such as heat, cold, high salinity, low salinity, and drought. This can also be related to cases of mass mortality in the sea.

In summary, it would appear that excess heat from the substrate was the cause of the death of Least Tern chicks along the Gulfport beach in 1980.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

A Marine Midge from the Gulf of Mexico

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DOI: 10.18785/grr.0702.09

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Howard, R. 1982. A Marine Midge from the Gulf of Mexico. *Gulf Research Reports* 7 (2): 167-168.
Retrieved from <http://aquila.usm.edu/gcr/vol7/iss2/9>

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A MARINE MIDGE FROM THE GULF OF MEXICO

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ABSTRACT The distribution of the marine midge *Telmatogeton japonicus* Tokunaga (Diptera) is extended into the northwestern Gulf of Mexico. This is the first reported use of offshore oil and gas platforms by marine midges and the first occurrence of this typically rocky shore intertidal group in an offshore environment.

Larvae of non-biting midges in the family Chironomidae (Insecta: Diptera) are abundant in most types of aquatic habitats. The majority of species are found in fresh water where more than half the species of macroinvertebrates may be chironomids (Coffman 1978). Of the approximately 120 genera and over 5,000 species in the family, 12 genera represented by 50 species are marine (Hashimoto 1976). Marine chironomids have been observed on intertidal rocky shores, coral reefs, and sandy and muddy bottoms of which the majority are associated with algae on rocky shores (Hashimoto 1976, Neumann 1976). Geographically, most marine chironomids are found on islands and shorelines of the Pacific Ocean. In North America, most species are found on the west coasts of Canada and the United States with only three east coast species (Wirth 1952, Beck and Beck 1959, Morley and Ring 1971, Hashimoto 1976).

Prior to this study the only documented occurrences of marine midges in the Gulf of Mexico were three species, *Thalassomya bureni* Wirth, *Clunio marshalli* Stone and Wirth, and *Telmatogeton japonicus* Tokunaga, reported from Florida (Wirth 1952, Beck and Beck 1959). I observed and collected larvae, pupae, and adults of *Telmatogeton japonicus* Tokunaga from offshore oil and gas platforms at three locations in the northwestern Gulf of Mexico. Locations of these sites were (1) 50 km south-southeast of Galveston, Texas (Buccaneer Gas and Oil Field, latitude 28°52'N, longitude 94°42'N); (2) 80 km south of Cameron, Louisiana (29°04'30"N, 93°25'40"W); and (3) 180 km southeast of Galveston, Texas (27°52'23"N, 93°53'43"W). Observations and collections were made during (1) December and March 1978, and February and August 1979 at site 1; (2) August 1979 at site 2; and (3) April 1980 at site 3. Both adults and immature stages were present in each collection period.

Offshore platforms in the Gulf of Mexico represent a new type of habitat for marine chironomids as well as an extension of the known distribution for *T. japonicus*. This species has previously been found in Japan, Hawaii, Australia, New York and Florida (Wirth 1952, Beck and Beck 1959, Hashimoto 1976).

The following ecological observations are based primarily on observations made at site 1; the collections at sites 2 and 3 were single events with fewer ancillary data noted. Larvae and pupae were found in silken tubes attached to the steel structures of platforms above the water line and to barnacles (mostly *Balanus tintinnabulum*) 0-10 cm below the water line. Larvae and pupae were observed from the water line to a height of about 1.5 m where they were more dense among a black zone of encrusting algae, presumably blue-green. Below the water line, larvae and pupae were attached to barnacles and among short but dense growths of algae which were growing on barnacles. Adults seldom ventured more than 1 m above the water line except during periods of severe wave action (a few individuals were observed 3-4 m high on the platform during these occasions).

Specimens collected in this study were found among, or in the vicinity of, growths of algae including *Cladophora* sp., *Polysiphonia* sp., *Enteromorpha* sp., and others. Wirth (1947) noted that most marine species of *Telmatogeton* prefer algae-covered rocks as habitat in fairly heavy surf. Each species has been associated with a dominant alga. Tokunaga (1935) noted that *T. japonicus* was always found between the tide marks on hard surfaces covered with three species of green algae—*Enteromorpha compressa*, *Ulva pertusa*, and *Monostroma* sp. Larvae in Hilo, Hawaii, were found on boulders near the outlet of a bay-front storm sewer where there was a heavy growth of *Ulva* sp. and *Enteromorpha* sp. (Wirth 1947).

On one occasion I observed spring-migrating warblers, which had apparently stopped to rest at the platforms at site 1, feeding on the adult midges. Predators of marine midge larvae have been reported to be shore crabs and tide-pool fish, and the adults were found to be prey to marine striders and mites (see review by Hashimoto 1976).

ACKNOWLEDGMENTS

I thank Willis W. Wirth (research entomologist, Systematic Entomology Laboratory, U.S. Dept. Agriculture, c/o U.S. National Museum) for taxonomic verification and suggestions on mechanisms of dispersal of the species.

This work is a result of research sponsored by the Environmental Protection Agency and Department of Com-

merce, National Marine Fisheries Service, Southeast Fisheries Service, Southeast Fisheries Center, Galveston Laboratory under Contract Numbers NA79-GA-C-00026 and NA80-GA-C-00057.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

Effects of Storms on Rice Rats Inhabiting Coastal Marshes

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DOI: 10.18785/grr.0702.10

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Recommended Citation

Wolfe, J. L. 1982. Effects of Storms on Rice Rats Inhabiting Coastal Marshes. Gulf Research Reports 7 (2): 169-170.
Retrieved from <http://aquila.usm.edu/gcr/vol7/iss2/10>

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EFFECTS OF STORMS ON RICE RATS INHABITING COASTAL MARSHES

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ABSTRACT During 1979, three storms with winds in excess of 73 km/hr and tides up to 1.5 m above normal struck a section of the Mississippi coast where a population study of the rice rat, *Oryzomys palustris*, was in progress. There were no noticeable effects on population levels, and many individual animals survived the storms.

INTRODUCTION

The rice rat, *Oryzomys palustris*, is a semiaquatic mammal that occurs in wetland habitats throughout the southeastern United States. Throughout most of its range, *O. palustris* is the most abundant small mammal in coastal marshes. It is also the most common mammal on many offshore islands in the northern Gulf of Mexico (Negus et al. 1961; personal observation). The tidal marsh and insular habitats of rice rats are occasionally subjected to devastating storms; and yet the rats appear either to survive these storms or to rapidly recolonize immediately following them.

MATERIALS AND METHODS

Since January 1979 I have been monitoring a rice rat population on the northern shore of St. Louis Bay in Harrison County, Mississippi. Two study grids about 1 km apart have been live-trapped quarterly. These grids have trapping stations placed at 15-m intervals. A 300-mm square floating platform that rises and falls with the tides is placed at each station. Each sampling session consists of one day of prebaiting the platforms with a mixture of oatflakes, peanut butter and sardines followed by four or five days of live-trapping. One Sherman live-trap is used on each platform. All animals captured are weighed, sexed, checked for reproductive condition, marked by toe clipping, and released. The westernmost grid is 12 stations long and 4 stations deep. Its long axis parallels shore. Water depth on its southern edge is about 400 mm at normal high tide. The northern edge parallels the marsh-forest ecotone and it is dry at normal high tide. The other grid consists of 100 stations in a 10 x 10 pattern. It extends from the forest-marsh ecotone for 135 m out into the marsh. Although the grid is about 0.5 km from shore, the southern half is flooded to a depth of about 300 mm daily by overflow from tidal creeks in the area.

In the spring and summer of 1979 three storms had an impact on the area. A storm in mid-April produced a tide of 1 m above normal and winds gusting to about 40 knots.

Hurricane Bob struck the area on July 11 with a storm tide of 1.5 m and winds up to 64 knots. On August 12, the western edge of Hurricane Frederick passed through with 74-knot winds but no storm tides, as the winds were from the north.

The April storm and Hurricane Bob completely inundated both grids with a tidal surge that swept away all the trapping platforms and deposited them in the forest, 50-100 m to the north. The duration of these storm tides was 2-4 hrs.

RESULTS

Trapping results from sessions preceding and following the 1979 storms are given in Table 1. Data from both grids are combined. No significant weather events occurred during the same segment of 1980, and data from this period are provided for comparison. Since many factors other than storms affect survival between sampling periods, this comparison is of limited use, and no specific statistical tests are attempted. Populations were generally higher in 1980, especially toward the end of the year. It is clear, however, that the impact of these storms on the rice rat population was not devastating, and probably not significant. Population levels showed little if any decrease following

TABLE 1.

Effects of storms during 1979 on rice rat populations in a tidal marsh at Bay St. Louis, Mississippi.

Months of Trapping	Days Between Storm and Trapping	Major Storms		Captures ³	
		Tide ¹	Wind ²	Total	% Recaptures ⁴
Jan.	—	—	—	33(52)	N/A(67)
May	30	1.0	73	20(19)	18(12)
Aug.	34	1.5	117	23(35)	10(16)
Oct.	35	0	135	15(45)	9(31)

¹ Tides are given as meters above normal high tide.

² Winds are in km/hr.

³ Comparable data from 1980, when no storms occurred, are given in parentheses.

⁴ Recaptures are percent of population marked in previous trapping session.

the storms. The number of marked individuals surviving periods with storms was similar to the number surviving the same interval the following year when no storms occurred.

DISCUSSION

Rice rats are known to be adept swimmers and divers (Esher et al. 1978). A dense shrub zone of *Baccharis halimifolia*, *Myrica cerifera* and *Ilex* sp., in the marsh-forest ecotone of the study areas, could have provided refuge, even though the two tidal surges reported swept completely through and beyond these areas. Homing behavior of rice rats has not been studied but may be an important behavioral adaptation for animals displaced

by storms. Birkenholz (1963) reported that high water in inland marshes gave rice rats a competitive edge over cotton rats. While details of the behavioral mechanisms for surviving storms are largely unknown, it appears that these are an important component of the species' adaptation to the coastal marsh environment.

ACKNOWLEDGMENTS

I thank the National Oceanographic Data Center, Washington, D. C., for the data on tides and wind velocity. This work was incidental to research supported by Contract 14-16-0009-79-094 from the Patuxent Wildlife Research Center of the U. S. Fish and Wildlife Service.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

Records of *Zygopa michaelis* Holthuis, 1960 (Decapoda: Anomura: Albuneidae) from the Gulf of Mexico

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DOI: 10.18785/grr.0702.12

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Recommended Citation

Reames, R. C., R. W. Heard and T. S. Hopkins. 1982. Records of *Zygopa michaelis* Holthuis, 1960 (Decapoda: Anomura: Albuneidae) from the Gulf of Mexico. *Gulf Research Reports* 7 (2): 171-173.

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RECORDS OF *ZYGOPA MICHAELIS* HOLTHUIS, 1960 (DECAPODA: ANOMURA: ALBUNEIDAE) FROM THE GULF OF MEXICO

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ABSTRACT The albuneid mole crab, *Zygopa michaelis* Holthuis, 1960, which was originally described from Curaçao and recently reported from the Florida East coast (Gore and Becker 1977), is reported from the Gulf of Mexico off the Florida West coast. Of the seven specimens collected, six were taken in 38 m of water off Fort Myers and one in 42 m on the Florida Middle Ground. All seven specimens occurred in substrata composed primarily of calcareous sand.

Seven specimens of the albuneid sand crab *Zygopa michaelis* Holthuis, 1960 have been collected during a study of the macroinvertebrate fauna of the eastern Gulf of Mexico. Six of these specimens were taken from a station in 38 m of water off Fort Myers, Florida. The bottom at this station is composed of coarse calcareous (carbonate) sand. The seventh specimen was collected from 42 m of water in the Florida Middle Ground, where bottom sediments are composed primarily of fine calcareous sand with a large portion of shell fragments.

Five specimens were collected with a Capetown Dredge. This dredge consists of a rectangular, steel-framed opening, followed by a tapering, angle iron frame covered by 1 x 2 cm expanded metal. Inside this apparatus is placed a removable liner frame covered with 1.3 x 1.3 cm vinyl-coated hardware cloth. The dredge was towed along the sandy bottom at these stations for 10–15 minutes. The remaining two specimens were taken with a box coring device. The core samples taken had a sediment depth of 20 cm with bottom surface dimensions of 21.3 x 30.5 cm.

Zygopa michaelis Holthuis, 1960. (Figure 1)

Material Examined — 1 ♀, 7.7 x 9.2 mm (carapace length by carapace width); R/V "Columbus O. Iselin," 15 September 1975, 26°15'N, 82°58'W; box core; 38 m; Coll. Wayne M. Bock; GCRL 1116. 1 ♀, 8.3 mm damaged; vessel name not presently available, January or February 1976, 26°15'N, 82°15'W; box core; about 38 m; collector's name not presently available; GCRL 1117. 2 ♀♀, 7.9 x 9.4 and 7.9 x 9.7 mm; 1 ♂, 8.2 x 9.9 mm; M/V "Indian Seal," 22 August 1977, 26°24'55"N, 82°57'56"W; 100 x 120 cm Capetown Dredge; 37 m; Coll. T. S. Hopkins; DISL 6183–1505. 1 ♀, 7.5 x 9.1 mm; M/V "Java Seal," 23 October 1977, 26°24'59"N, 82°58'0"W; 100 x 120 cm Capetown Dredge, 38 m; Coll. T. S. Hopkins; USNM 184958. 1 ♀, 10.3 x damaged (approximately 6.4 mm); M/V "Indian

Seal," 5 February 1978, 28°29'46"N, 84°20'49"W, 100 x 120 cm Capetown Dredge; 42 m; Coll. T. S. Hopkins; DISL 6183–1504.

Our seven specimens from the eastern Gulf of Mexico agree with the original description by Holthuis (1960) and with specimens in the collections of the National Museum of Natural History (USNM 122644 and 168526) studied by Gore and Becker (1977). The color was, as noted by Holthuis (1960) and Gore and Becker (1977), ivory to chalky white with pilosity on the appendages ranging from yellow to golden brown. *Zygopa michaelis* is easily distinguishable from other species of American albuneids by their apparent lack of eyes, (seen to be small and fused on close examination), and by the distinct outline of the anterior margin of the carapace.

The range for *Zygopa michaelis* now extends from Curaçao, in the southern Caribbean, to southeastern Florida and the eastern Gulf of Mexico. We agree with Gore and Becker (1977) that the disjunct distribution is an artifact of collecting methods.

The two specimens taken by box core are deposited in the collection of the Gulf Coast Research Laboratory Museum (GCRL). One of the specimens (Fig. 1) taken by dredge off Fort Myers has been deposited in the collections of the National Museum of Natural History. The other dredge specimens from that station and the one from the Florida Middle Ground have been deposited in the Bureau of Land Management (BLM) Reference Collection at the Dauphin Island Sea Lab (DISL), Dauphin Island, Alabama.

Zygopa michaelis was originally described from Sint Michiels Baai, Curaçao, in the Netherlands Antilles. The 20 original specimens (14 ♀♀, 6 ♂♂) were taken in 1957 by suction dredge from fine white sand in about 4 m of water. The genus is distinguished by (1) eyes which are much reduced and fused or "yolk shaped," and by (2) presence of two submedian teeth on the anterior margin of the carapace which are separated by a concavity rather than a single median tooth. The color is noted to be chalky white without iridescence (Holthuis 1960).

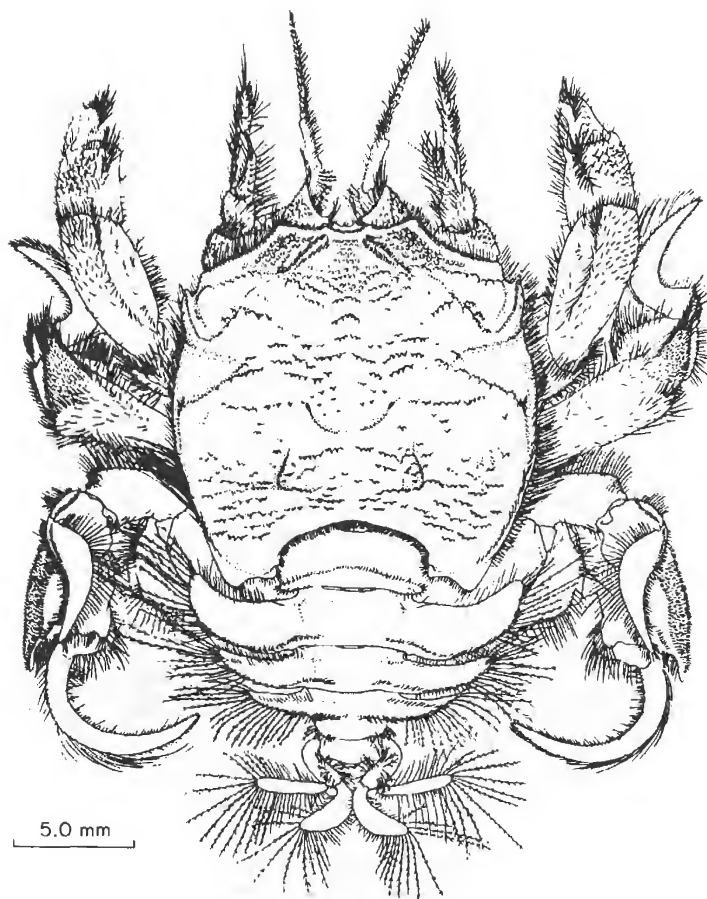


Figure 1. *Zygopa michaelis* Holthuis, 1960. Female (USNM 184958) from off Fort Myers, Florida, U.S.A.

A second species, *Zygopa nortoni* Serene and Umali, 1965, described from the Philippines, with the type specimen collected from Bantangas Bay, Luzon, is reported to differ from *Z. michaelis* primarily in eye morphology, but also in the number of joints on the antennular flagellum and in cheliped morphology (Serene and Umali 1965).

Gore and Becker (1977) extended the range of *Z. michaelis* to the southeast coast of Florida, constituting a 2100-km range extension. Of the five specimens they reported, one female was collected in 1950 from 55–73 m of water off Palm Beach, Florida; and it remained unidentified until after Holthuis' description of the species in 1960. The four other specimens were collected in August 1976 from 55 m of water off Miami, Florida. Those specimens were collected with a tumbler dredge, while the collection method for the Palm Beach specimen was not noted.

The following additional measurements are the same em-

ployed by Gore and Becker (1977) for their material. These measurements are provided in order of collection date for the Fort Myers and Florida Middle Ground specimens: fronto-orbital, ♀, 0.9; ♀, 1.2; ♀, 1.1; ♂, 1.2; ♀, 1.2; ♀, 1.0; ♀, 1.3 mm; intramedial tooth width, ♀, 3.3; ♀, 3.7; ♀, 3.4; ♂, 3.6; ♀, 3.7; ♀, 3.3; ♀, 4.8 mm; anterolateral width, ♀, 7.7; ♀, 8.6; ♀, 7.8; ♂, 7.9; ♀, 8.1; ♀, 7.7; ♀, 10.8 mm; antero-lateral tooth width, ♀, 8.6; ♀, 9.5; ♀, 8.7; ♂, 8.8; ♀, 9.0; ♀, 8.4 mm; ♀, damaged.

A number of other crustaceans were collected in the two box core samples that contained *Z. michaelis*. These included a stomatopod (*Eurysquilla plumata* Bigelow), tanaidaceans (*Leptochelia* sp. and *Apseudes* sp.), cumaceans (*Cyclaspis unicornis* Calman, *Campylaspis* sp. and *Cumella* spp.), amphipods (*Ampelisca agassizi* Judd, *Photis melanicus* McKinney, *Unciola serrata* Shoemaker and *Lysianopsis* sp.) and a caridean shrimp (*Automate* cf. *evermanni* Rathbun).

ACKNOWLEDGMENTS

We wish to thank Drs. Austin B. Williams and Raymond B. Manning for the loan of specimens from the USNM for comparative purposes and Drs. A. B. Williams, Robert H. Gore, and L. B. Holthuis for reviewing the manuscript.

Special thanks are due Linda Lutz for the biological illustration. The collection of our specimens was made possible by BLM contract number AA550-CT7-34 to Dames and Moore (dredge samples) and BLM contract number 08550-CT5-30 to the State University System of Florida (box core samples).

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

Elevational Variations in the Lowest Limit of *Spartina* Colonization in a Virginia Salt Marsh

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Reidenbaugh, T. G., W. C. Banta, S. Mendoza, R. P. Strieter and M. Varricchio. 1982. Elevational Variations in the Lowest Limit of *Spartina* Colonization in a Virginia Salt Marsh. *Gulf Research Reports* 7 (2): 175-178.
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ELEVATIONAL VARIATIONS IN THE LOWEST LIMIT OF *SPARTINA* COLONIZATION IN A VIRGINIA SALT MARSH

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ABSTRACT Elevations of lowest colonization of smooth cordgrass, *Spartina alterniflora*, were surveyed along the edge of a juvenile salt marsh at Wallops Island, Virginia. This lowest limit of *Spartina* varied over one-third of the local mean tidal range, with lowest occurrences between mean low water and mean low water neaps. Four geographical factors appeared to influence the lowest limit of *Spartina*: (1) tidal scouring in areas where tidal channels were constricted, (2) scalloping of the marsh edge over a sloping substrate, (3) patterns of historical development of the marsh, and (4) ice scouring of previously colonized *Spartina* over winter. Marsh edge scallops occurred only in areas of former *Spartina* thatch islands, and probably resulted from lateral spreading of those islands.

INTRODUCTION

Vegetation boundaries may be used to set management boundaries in salt marshes, so it is especially important to accurately measure the distribution of plants within marshes. In salt marshes of the East Coast of the United States, the smooth cordgrass, *Spartina alterniflora*, is usually the dominant rooted plant, or only rooted plant, of regularly flooded zones. Even so, detailed study of *Spartina's* lower elevational limit is lacking; it has been described generally as occurring between the elevations of mean low water and mean tide level (Chapman 1940, Broome et al. 1974). For the present study, we measured the very lowest limit of *Spartina*, i.e. elevation of the farthest-seaward *Spartina* along its edge of colonization, in a single marsh.

METHODS AND MATERIALS

This study was conducted in the Project IBIS (Intensive Biometric Intertidal Survey) study site in the Cow Gut Flat salt marsh on northern Wallops Island, a Virginia barrier island. This is a juvenile marsh (according to the classification of Redfield 1972), dominated by tall and medium growth form *Spartina* (to about 2.0 m), on generally unidirectionally sloping substrate from bay to upland, with no mature tidal creeks (described in Reidenbaugh and Banta 1980; Reidenbaugh, in press). Tidal data at the site have been estimated from a series of tide staff observations compared to a tide gauge record from Mosquito Creek, Virginia, 8 km away (Reidenbaugh 1978). Mean tidal range is 0.8 m; salinity of tidal water if from 30.0 to 32.5 ppt.

Elevations of the lowest limit of *Spartina* were surveyed with transit and stadia along the entire length of the Cow Gut Flat marsh from Gunboat Point, near Chincoteague Inlet, to Cow Gut, 1.5 km toward Chincoteague Bay. One hundred forty-nine stations were surveyed, 21 of them

below parallel rows of permanent stakes 10 m apart and roughly perpendicular to the marsh edge, and 128 stations located by cloth tape every 10 m along the marsh edge in both directions from the stakes. At each station, the stadia was held flush with the sediment at the single farthest-seaward *Spartina* shoot. Transit shots were limited to about 100 m. Levels were read to the nearest 1 mm and converted to absolute elevations relative to the National Geodetic Vertical Datum (NGVD) by running level lines to a National Oceanic and Atmospheric Administration bench mark 1.5 km away. All surveying was done from June 27 to July 12, 1978.

A map of the Cow Gut Flat marsh was drawn from color infrared aerial photographs (Kodak film 2443) taken July 19, 1976. Transparencies of 1:2,000 original scale were enlarged to 1:1,333 on a reflecting projector. Portions of five frames were combined into one map. The lowest limit of *Spartina* was traced along the marsh edge as the division between reddish tones of vegetation and bluish tones of bare sediment. The upper limit of the marsh was drawn along the saltbush line of *Iva frutescens* and *Baccharis halimifolia*.

RESULTS AND DISCUSSION

Elevations of the lowest limit of *Spartina* in the study site ranged from -0.356 to -0.095 m NGVD (Fig. 1; elevations of tidal data are mean low water, -0.387 m; mean low water neaps, -0.311 m; and mean tide level, 0.009 m NGVD). Observed emergence at low water levels confirmed that this variation was in *Spartina* colonization, rather than local variations in tidal data. There were relatively frequent occurrences of the lowest limit of *Spartina* near mean low water neaps, though the distribution of occurrences was skewed toward higher elevations. The mean elevation of the lowest limit was -0.274 m (standard deviation \pm 0.045 m); the median elevation was -0.287 m.

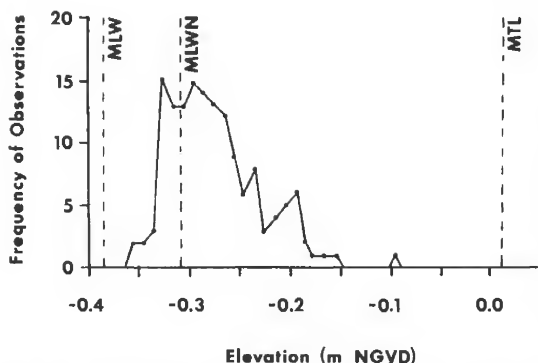


Figure 1. Elevational distribution of the lowest limit of *Spartina* (relative to the National Geodetic Vertical Datum, NGVD), compared to tidal data of mean low water (MLW), mean low water neaps (MLWN), and mean tide level (MTL).

Much of the elevational variation in the lowest limit of *Spartina* appeared to be related to geography of the marsh (Fig. 2). We hypothesize that four geographical factors influence the lowest limit of *Spartina* here: (1) tidal scouring, (2) scalloping of the marsh edge, (3) patterns of historical development of the marsh, and (4) ice scouring.

Tidal Scouring

Elevations of the lowest limit of *Spartina* increased in areas where tidal channels were constricted, where current velocities and tidal scouring likely increased. Thus, the lowest limit increased opposite a large marsh island about 100 m offshore (between letters C and L, Fig. 2). This island accreted alongside the former main tidal channel through Chincoteague Inlet (which was blocked by the modern growth of Gunboat Point; Reidenbaugh 1978), and constricted the remnant channel along Cow Gut Flat. Similarly, relatively high elevations of the lowest limit of *Spartina* farther southeast also corresponded to constrictions of this same channel by the inner shoreline of Gunboat Point (A and B, Fig. 2).

The lowest limit of *Spartina* increased sharply at the mouth of Cow Gut (U, Fig. 2), where tidal flow from bay to marsh was greatly constricted. It also increased sharply toward mouths of present or former inlets between *Spartina* thatch islands east of Cow Gut (thatch islands, N, P, and S, Fig. 2; inlet, M; former inlet, Q). Thatch islands are isolated stands of *Spartina* from seeding or ice-raftering of rhizomes (Redfield 1972). The oldest of these thatch islands (S, Fig. 2) was first colonized about 1955 (Reidenbaugh 1978).

Scalloping

At many places, the marsh edge was contoured into a series of scallops with alternating concavities and convexities; individual scallops were from 10 to 60 m long. Elevations of the lowest limit of *Spartina* were consistently lower

along convexities, and higher in concavities (D, E, G, H, I, K, and L, Fig. 2). It thus seems likely that the scallops resulted from variations in lateral spreading of *Spartina* on a fairly uniformly sloping substrate, rather than from topographical variations of the substrate.

Coalescence of thatch islands resulted in scalloping near Cow Gut, and elevations of the lowest limit of *Spartina* varied along these scallops as they did elsewhere (O, R, and T, Fig. 2). Variations here probably reflected the lateral spreading of *Spartina* from initial centers of colonization; *Spartina* which spread seaward grew downslope to lower elevations. Radii of the roughly circular thatch islands suggest that they had spread at an average maximum of about 1 m/yr in all directions. The scallops to the southeast of these existing thatch islands probably resulted from similar spreading of former thatch islands which colonized before 1955 atop a longshore sandbar offshore from the marsh edge (Reidenbaugh 1978). *Spartina* has since filled the area behind the bar.

Historical Development

Patterns of the lowest limit of *Spartina* varied relative to a geographical division in the marsh. This division occurred where a projection of relatively high land (F, Fig. 2) resulted in different rates of marsh development on its northwest and southeast sides. Historically, this projection sheltered Cow Gut Flat to its northwest from waves and currents of the former channel through Chincoteague Inlet (Reidenbaugh 1978). Marsh had colonized there since 1949 (Reidenbaugh 1978), and was presently up to 130 m wide. Much of the seaward colonization was by *Spartina* thatch islands. The marsh edge was scalloped all along this area.

Southeast of the projection, the shore was unsheltered from the former channel. Marsh had only colonized since 1966 (Reidenbaugh 1978), and it was presently only 40 m at its widest. There were no thatch islands there, instead the marsh had grown by downslope spreading from high marsh. No scallops occurred, presumably because they develop from thatch islands. In this area of the marsh, the lowest limit of *Spartina* may have been more affected by topographical variations of the substrate.

Ice Scouring

The lowest limit of *Spartina* may have been increased locally by winter ice scouring of previously colonized *Spartina*. We observed ice scouring that completely denuded one area of *Spartina* shoots and rhizomes on January 24–25, 1977 (J, Fig. 2); the lowest limit of *Spartina* was highest there of all areas surveyed. Such ice scouring may partly account for the skewness in the distribution of the lowest limit of *Spartina* toward higher elevations (Fig. 1).

Elevations of the lowest limit of *Spartina* along the edge of the Cow Gut Flat marsh varied considerably over short distances, especially along present or former thatch islands.

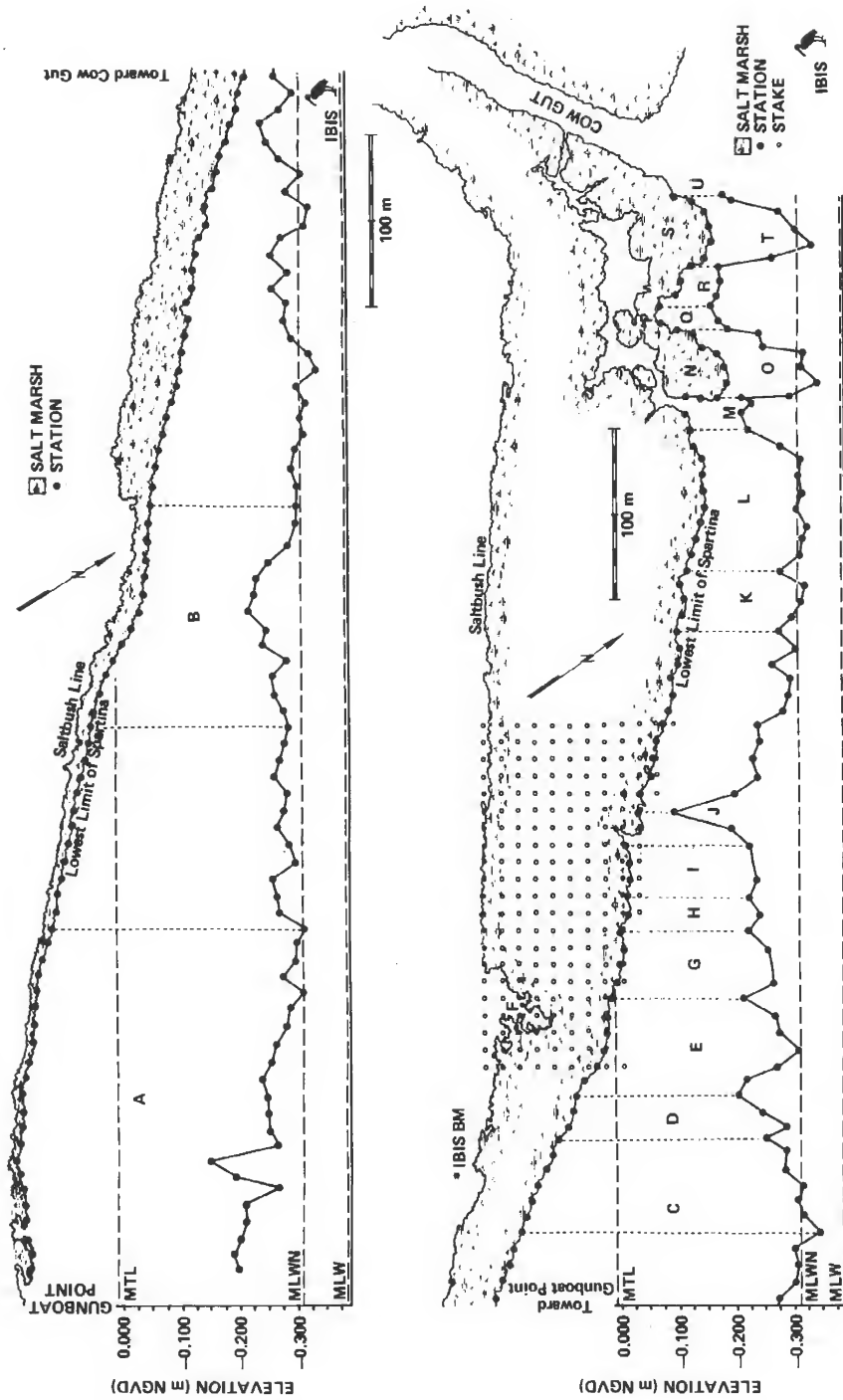


Figure 2. Elevations of the lowest limit of *Spartina* along the Cow Gut Flat salt marsh.

Much of this variation reflected differences in initial colonization and spreading of *Spartina* in this juvenile marsh. However, as the marsh matures, we expect these variations to become less significant as much of the farthest-seaward *Spartina* approaches its absolute physiological lowest limit. Patterns of historical development of the marsh and scalloping will be much less important factors than they are now. Instead, the mature marsh edge will be determined by the absolute physiological lowest limit of *Spartina*, tidal scouring, ice scouring, and possibly other factors. We did not determine the absolute physiological lowest limit of *Spartina* here, but it is at least as low as midway between mean low water and mean low water neaps, where we made

several observations. Therefore, in regional management planning for *Spartina* marshes, presently uncolonized tidal flats contiguous with expanding *Spartina* marshes should be considered as potential *Spartina* marshes to elevations at least as low as midway between mean low water and mean low water neaps.

ACKNOWLEDGMENTS

This study was part of The American University's Project IBIS, and was funded by a grant from the Griffis Foundation. Aerial photographs were generously provided by the National Aeronautics and Space Administration-Wallops Flight Center.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

Size-Specific Emergence of the Marsh Snail, *Littorina irrorata*: Effect of Predation by Blue Crabs in a Virginia Salt Marsh

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DOI: 10.18785/grr.0702.14

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Stanhope, H. S., W. C. Banta and M. H. Temkin. 1982. Size-Specific Emergence of the Marsh Snail, *Littorina irrorata*: Effect of Predation by Blue Crabs in a Virginia Salt Marsh. Gulf Research Reports 7 (2): 179-182.
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SIZE-SPECIFIC EMERGENCE OF THE MARSH SNAIL, *LITTORINA IRRORATA*: EFFECT OF PREDATION BY BLUE CRABS IN A VIRGINIA SALT MARSH

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ABSTRACT Marsh periwinkles of 5 to 7 mm in shell height were eaten regularly by blue crabs. Fractures marking unsuccessful crab attacks were present in about 25% of medium-sized (10–16 mm) snails and over 60% of larger snails (over 16 mm). Medium-sized snails, subject to predation, leave the water more frequently than larger snails, but only about a quarter of the snail population leaves the water during high tide. We found no evidence that the snails leave the water because they sense blue crabs in the water.

INTRODUCTION

The marsh periwinkle *Littorina irrorata* (Say) is a grayish gibbous, intertidal snail common in salt marshes from New York to Texas. It is believed to be a grazer, feeding largely on plant detritus and epipellic algae (Odum and Smalley 1959; Stiven and Kuenzler 1979). According to Bingham (1972) and Hamilton (1976, 1978), periwinkles are effectively supratidal; they avoid submergence by crawling upward out of the water when inundated. Bingham (1972) attributed the absence of snails in barren areas to "reluctance of the species to remain submerged." Bleil and Gunn (1978) demonstrated that this response is not caused by threat of drowning; the snails can survive long periods under water. Hamilton (1976) attributed the avoidance of submergence to predation by the blue crab *Callinectes sapidus* Rathbun, which enters the marsh with the flood tide and preys on periwinkles. Crist (1979) found that a size gradient exists in periwinkles; larger individuals occur more frequently than smaller snails at lower elevations in the marsh. He attributed this in part to differential predation on smaller snails by blue crabs, which are more abundant at lower elevations.

Preliminary observations on a study site at Wallops Island, Virginia, indicated that a substantial majority of specimens of *L. irrorata* remained under water at high tide, despite an abundance of emergent vegetation. That observation was an obvious contradiction to the behavior of *L. irrorata* in an aquarium—all snails crawl out of the water immediately (Bingham 1972).

We noticed also that smaller snails tended to be more abundant out of water on stalks of vegetation than in the water. We reasoned that there may be a size-specific difference in the response of snails to submergence because of differential predation on smaller snails relative to larger ones.

The purpose of this paper is to quantify the size-specific

proportions of snails which emerge from the water at high tide in the field, and to test the hypothesis that blue crab predation may influence those proportions.

MATERIALS AND METHODS

The study site was a juvenile sloping foreshore marsh located on Cow Gut Flat at the north end of Wallops Island, near Chincoteague, Virginia. Drainage at low tide is nearly complete, and freshwater input is limited to rainfall and groundwater discharge. No tidal creeks or primary pans are present. Tall and medium vigor *Spartina alterniflora* (Loisel) predominate. *Salicornia* spp. is abundant at some higher elevations; the highest elevations are dominated by marsh elder, *Iva frutescens* (Linnaeus) (Reidenbaugh and Banta 1980).

Tidal wrack, consisting primarily of dead stalks of *S. alterniflora*, formed dense mats, which were rafted into the site during abnormally high tides (Reidenbaugh and Banta 1980). Vegetation compressed beneath stranded mats often is partly or completely killed, and in the most severe cases, secondary bare areas formed.

Field experiments were conducted within a 17,000-m² study site marked by wooden stakes placed at 10-m intervals from below mean low water to above mean high water. The study site has been named the Intensive Biometric Intertidal Survey (IBIS) marsh (Reidenbaugh and Banta 1980).

To determine the size distribution of *Littorina irrorata* in the IBIS marsh survey grid, 30 sampling points were located relative to stakes, using computer-generated random numbers. Elevations at each collecting site were determined by linear interpolation among the four surrounding stakes. Stake elevations were determined by transit relative to Bench Mark IBIS, +1.427 m National Geodetic Vertical Datum (NGVD). A 1-m² quadrat was centered at each of the sampling points at or near the time of low tide between 16 and 18 July, 1979. The weather during this time was uniformly sunny and warm, with temperature maxima near 30°C. All marsh periwinkles were collected, counted, measured to the nearest 1 mm shell height, and returned to the same quadrat.

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Manuscript received February 8, 1982; accepted July 28, 1982.

The proportion of emergent snails was determined by returning to the same 30 quadrats at high tide. Predicted high tides at Chincoteague Point, 1 km away, were used. United States Geodetic Survey tide tables predict tides at the IBIS marsh site within less than 2 mm (Reidenbaugh 1978). A 1-m² wood frame was floated on the surface of the water, and emergent snails on stems and blades of emergent vegetation were counted and measured. Water depth and average height of the highest stalks were estimated using a meter-stick; height of emergent vegetation was estimated as the difference between those two values. Variation in plant density among sites was relatively constant (Reidenbaugh 1978).

To study crab predation on snails, blue crabs of various sizes were netted near the IBIS marsh and starved about 24 hours in separate 85-liter aquaria with filter beds of crushed oyster shell; crabs were then offered snails of various sizes. Observations and photographs were made of the crabs' behavior, and damage to the snails was noted.

For studying fractures in shells, 330 snails were removed at low tide from five randomly selected quadrats at various elevations in the study site between 0.173 and 0.434 NGVD. Individuals were measured and examined for repaired fractures in the shell, and for evidence of severe shell erosion which might obliterate visible marks.

To determine if the presence of crabs in the marsh had an effect on the behavior of the periwinkles, three crabs were placed in a plastic mesh bag. Five such bags were staked in the center of five of the 30 sampling quadrats on an incoming tide. At high tide emergent snails were measured and counted.

RESULTS AND DISCUSSION

Figure 1 illustrates the proportion of snails emergent at low tide at 30 randomly selected quadrats. Of the 1,722 snails present in all quadrats at low tide, 491 (29%) were emergent at high tide. No significant correlation was found between the proportions of snails emergent at high tide and the absolute elevation of the marsh surface ($n=30$, $r=0$, $p[t]=0.977$). This finding confirmed our visual observations that snails tended to be scattered fairly evenly along vegetation stalks and that they were fairly indifferent to submergence.

Large snails (19 mm and greater in height) were about twice as likely to be submerged as smaller snails (12–18 mm) (Fig. 2). Snails less than 12 mm in height were present in relatively low numbers (fewer than 20) and were not considered further.

We attempted to determine if the relative submergence of *L. irrorata* might vary geographically. We reasoned that predation of crabs might be heavier farther south, selecting for an adaptive cline in water avoidance—that is, more southerly snails might be more subject to predation and therefore be selected to spend more time out of water than

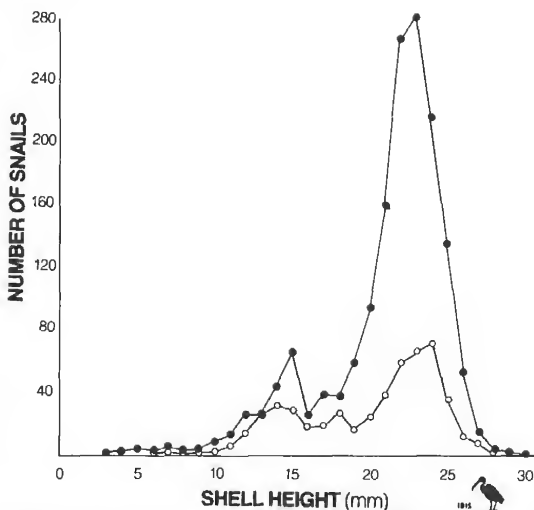


Figure 1. Size-frequency distribution of snails from randomly selected 1-m² quadrats. Closed dots represent all snails counted at low tide; open circles indicate snails emergent at high tide.

their more northerly conspecifics.

We made a cursory inspection of a *Juncus* marsh in which *L. irrorata* was abundant, at Ocean Springs, Mississippi, during March 1979. More snails appeared to be under water than out of it. In a study of a marsh in Georgia, four quadrats were selected, each at a different elevation. Eighty snails were counted when the tide was out; 36 (45%) were counted out of the water on the stalks when the tide was in. We conclude that individuals of *L. irrorata* spend a

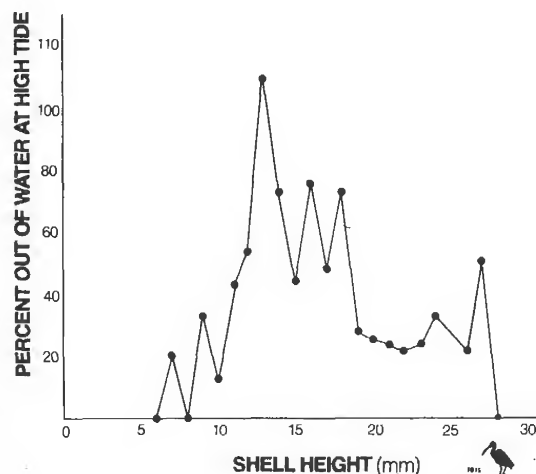


Figure 2. Percentage of snails out of the water on vegetation stalks at high tide plotted against shell length. Conventions as in Figure 1.

substantial part of their lives under water, at least through most of the animal's range.

Blue crabs attacked specimens of *L. irrorata* by breaking away bits of the outer body whorl. This process was described in detail by Hamilton (1976). Crabs did not attack snails with a shell height less than about 5 mm, presumably because the snails were too small to be noticed or too small to trouble with. If an attack on a snail succeeded, i.e., if the crab ingested significant meat from the shell, the entire snail was usually eaten and the shell reduced to small fragments.

Our data suggests that crabs may learn to eat periwinkles. One large crab (carapace width, 15 cm) refused periwinkles of all sizes until we drilled two small holes in the shell near the aperture of a 20 mm snail. The holes allowed the crab to grasp the shell securely and eventually to break it to pieces. Thereafter, the crab was an active predator on *Littorina*, regularly eating snails up to 16 mm long.

The largest undamaged snail we observed being crushed by any crab was 17 mm, almost the same size (16 mm) reported by Hamilton (1976).

Occasionally, crabs in aquaria abandoned their attempts to open periwinkle shells after they had only chipped the aperture. We observed similar fracture marks on live snails in the field; those fractures were usually preserved as growth discontinuities some distance from the aperture.

The proportion of snails whose shells were marked by fractures varied with size (Fig. 3). No snails with a shell length of less than 10 mm had fractures. Relatively low proportions (about 25% of medium-sized snails, 12–16 mm) contained fractures. We attribute the low proportion of fracture marks among small snails to the way that blue crabs eat periwinkles. Snails too small for blue crab predation (under about 5 mm), obviously will be free of fracture marks. Snails between 5 mm and about 10 mm were eaten

almost each time they were attacked by blue crabs. In these cases the shells are reduced to small, unrecognizable shell fragments. The proportion of snails with fracture marks on their shells increased dramatically to about 60% in snails 17 to 20 mm in height, then dropped steadily among snails over 22 mm in height. The largest snails examined (26–27 mm) showed no signs of fractures. The decline in proportion of fractured shells among the largest snails is probably due to shell erosion; the proportion of the shell which was badly eroded correlated strongly with size (Fig. 3).

We found no evidence to indicate that *L. irrorata* sense blue crabs in the water during high tide. A t-test showed no significant difference in snails out of water between control trials and trials in which blue crabs were restrained in the experimental quadrats ($n=5$, $t=0.463$, $p[t]=0.492$).

SUMMARY AND CONCLUSIONS

1. On the average, marsh periwinkles at our study site in Virginia were distributed on the marsh floor or along vegetation stalks. We found no significant correlation between the absolute elevation of the marsh surface and the proportion of snails out of water at high tide. Most snails appeared to be relatively indifferent to submergence by the tide. Preliminary evidence suggests that the same is true for *L. irrorata* in Georgia and Mississippi.

2. Snails of about 12 to 18 mm in shell height spend proportionally more time out of the water than larger snails (19 mm and over). The change in behavior that occurred when snails reached about 18 to 19 mm in height may be an adaptation to crab predation, because smaller snails, less than about 17 mm, can be crushed and eaten by blue crabs, whereas larger snails were relatively safe.

3. Blue crabs were almost always successful in attacking snails of 5 to 15 mm in height; the shells were reduced to small fragments. Unsuccessful attacks, recorded as fractures in shells, were common on individuals over 10 mm in height. Over 60% of larger snails were probably attacked unsuccessfully.

4. We found no evidence to indicate that *L. irrorata* leaves the water in response to the presence of blue crabs nearby.

ACKNOWLEDGMENTS

We thank Rhoda Twombly, Zaida Gutierrez, Natashs Brock, Robert Streiter, Thomas Reidenbaugh, Keith Whitentstrom, and Donald Bonyai for help in the field. Sheree Cohn made the field observations in Georgia. The work was made possible by the staff of the National Aeronautics and Space Administration; special thanks are due Robert Krieger, Director. Mr. Dick White and Dr. Kenneth Turgeon of the Marine Science Consortium helped greatly with field support.

This paper was written by undergraduate students supervised by W. C. Banta, Director of IBIS. IBIS contribution 15.

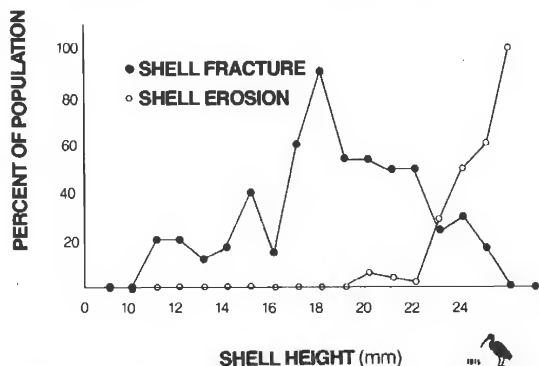


Figure 3. Percentage of the *L. irrorata* population showing evidence of predation as healed fractures in the shell, plotted against shell length. Also shown is the frequency of obvious shell erosion. The two data points at 27 mm are based on the same single specimen. Other data points are based on numerous individuals.

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Gulf Research Reports

Volume 7 | Issue 2

January 1982

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DOI: 10.18785/grr.0702.15

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Walker, R. L. 1982. The Gastropod *Thais haemastoma* in Georgia: *T. h. floridana* or *T. h. canaliculata*?. Gulf Research Reports 7 (2): 183-184.

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THE GASTROPOD *THAIS HAEMASTOMA* IN GEORGIA: *T. H. FLORIDANA* OR *T. H. CANALICULATA*?

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ABSTRACT In the southeastern United States, the snail *Thais haemastoma* has traditionally been subdivided into two subspecies according to the snail's locale, size of shell, number and size of spines, and depth of suture. Only *Thais haemastoma floridana* is supposed to occur in Georgia; since *Thais haemastoma canaliculata* is supposedly restricted to the Gulf of Mexico region. In Georgia, specimens fitting the description of both subspecies are common. The author concurs with the conclusions of Butler (1953) and Gunter (1979) in that the subspecies nomenclature is invalid and that they are merely ecological variants.

In the southeastern United States, the genus *Thais* (Family Muricidae) is comprised of two subspecies: *Thais haemastoma floridana* (Conrad, 1837) and *Thais haemastoma canaliculata* (Gray, 1839) which are differentiated by locale, shell length, number and size of spines, and depth of the suture (Abbott 1974). Previous studies indicate that the Florida Rock-shell *Thais haemastoma floridana* ranges from North Carolina to the West Indies and along the Central American coast to Trinidad; Hay's Rock-shell *Thais haemastoma canaliculata* ranges from the west coast of Florida to possibly the northern coast of Mexico (Clench 1947). The drills differ in shell length, with *T. h. floridana* reaching 75 mm and *T. h. canaliculata* reaching 105 mm. *T. h. floridana* has two or more rows of weak shoulder nodules, while *T. h. canaliculata* has two rows of strong shoulder nodules. *T. h. canaliculata* has a more deeply channeled suture (Clench 1947).

In Georgia, *Thais haemastoma* is uncommon (Walker 1981, Walker et al. 1980, Hoese 1969), although it may be common in specific areas (Hoese 1969). In a recent drill survey of Wassaw Sound, Georgia (Walker 1981), *Thais haemastoma* was found inhabiting oyster bars in two areas: approximately 500 meters north of the mouth of Cabbage Creek, Cabbage Island, and at the Deadman Hammock area, Wassaw Island. The snails were found preying on oysters at or near the mean low water mark in the more saline areas ($S \times 10^{-3} > 18$) of Wassaw Sound. Due to the rarity of the snail in Georgia, it does not represent any serious threat to the oyster fishery as it does in more southern waters (Butler 1953).

According to locale, the Georgia population should be *T. h. floridana* because *T. h. canaliculata* is restricted to the Gulf of Mexico. However, many of the specimens found during the drill survey of Wassaw Sound best fit the description of *T. h. canaliculata*. For example, 11 out of 23 shells were greater than 75 mm in length, the maximum length

cited for *T. h. floridana*. Of these, five were over 80 mm, one was over 90 mm and one was 105 mm in length. The shoulder nodule(s) varied in size and number: 22% with two strong shoulder nodules, 26% with one strong and one weak nodule, 22% with two weak nodules, and 26% with only one weak nodule. The remaining shells were heavily infested with *Cliona* and not enough of the shell remained for adequate analysis. Furthermore, Hoese (1969) found in Georgia (N=62) 43 *Thais* shells over 79 mm, nine over 89 mm and two over 99 mm. The largest reached 101 mm. Chesnut (1955) found *Thais* reaching 83 mm in North Carolina. Unfortunately, no descriptive characteristics of the shells were given by either Chesnut (1955) or Hoese (1969).

Specimens collected by the author from Shell Island, Florida, south of Mexico Beach, Florida, were also examined. Of these (N=7), 29% had two strong shoulder nodules, 14% had two weak shoulder nodules, 29% had one weak shoulder nodule and 29% had no shoulder nodules. According to locale, they should all be classified as *T. h. canaliculata*; however, most, due to the absence of two strong shoulder nodules on the majority of the shells collected, fit the description of *T. h. floridana*.

Mayr (1963) defines a subspecies as "an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species" (p. 672). The occurrence of shells resembling *T. h. canaliculata* in Georgia and shells resembling *T. h. floridana* in the Gulf of Mexico region show that the populations (Gulf vs. Atlantic) are not taxonomically different. Furthermore, Butler (1953) reports finding specimens of both subspecies in Pensacola, Florida, as well as in Barataria Bay, Louisiana. Gunter (1979) reports specimens of both subspecies in Apalachicola Bay, Florida.

One can explain the presence of shells resembling *T. h. canaliculata* in Georgia in three ways: (1) that *T. h. canaliculata* was introduced into Georgia waters from the Gulf region; (2) that the Georgia population being taxonomically distinct from *T. h. floridana* should be given another sub-

species status; or (3) that the snails are *Thais haemastoma* and that subspecies nomenclature is invalid. The first is possible considering that transplantation of oysters infested with drills is the major factor in drill (*Urosalpinx*) dispersal in more northern waters. However, no known instances of transplantation of oysters from the Gulf region to Georgia is known. The second, in view of specimens fitting the description of both subspecies occurring in five distinctly separate areas seems unwarranted. The third case is most likely. It would appear that *T. h. floridana* and *T. h. canali-*

culata are ecological forms and that subspecies status is unwarranted. Therefore I agree with Gunter's (1979) statement, "In the meantime it would seem the remaining conservative course is to use the only indubitably valid name, *Thais haemastoma*."

ACKNOWLEDGMENTS

The author wishes to thank Drs. G. Gunter, C. Humphrey, and K. R. Tenore for reviewing the manuscript. The work was funded by the Georgia Sea Grant Program.

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